

THE EVOLUTION OF THE AUSTRALIAN MARSUPIALS

by

A.M. Pearse B.Sc.Gen.Sc.

A preliminary reading thesis submitted as
qualification for the Degree of Master of
Science.

University of Tasmania

March, 1976.

CONTENTS

	<u>Page</u>
Abstract	i
Introduction	ii
 <u>SECTION 1 - ORIGIN OF AUSTRALIAN MARSUPIALS</u>	
Origin of Marsupials	1
Relationships of Marsupials to Other Mammals	1
Fossil Evidence	11
Dental Evidence	12
Reproductive Evidence	14
Summary	20
Dispersal of Marsupials	24
 <u>SECTION 2 - THE AUSTRALIAN RADIATION</u>	
Classification of Major Groups of Marsupials	28
Summary	29
Evolution of Marsupials within Australia	30
Summary	38
Superfamily Dasyuroidea	39
Family Dasyuridae	40
Summary	49
Family Thylacinidae	49
Family Myrmecobiidae	51
Order Peramelina	52
Origin of the Peramelina	52
Evolution within the Peramelina	56
Summary	62

CONTENTS

	<u>Page</u>
Evolution of the Diprotodonta	64
Origin of Diprotodonty	64
Origin of Diprotodonta	66
Evolution within the Diprotodonta	66
Superfamily Phalangeroidea	67
Origin of the Phalangeroidea	67
Summary	70
Family Wynyardidae	72
Family Burramyidae	73
Summary	78
Family Petauridae	80
Summary	83
Family Phalangeridae	85
Summary	87
Family Thylacoleonidae	89
Family Macropodidae	91
Subfamily Potoroinae	91
Subfamily Sthenurinae	96
Summary	98
Subfamily Macropodinae	100
Superfamily Vombatoidea	105
Family Vombatidae	105
Family Phascolarctidae	107
Family Diprotodontidae	107
Superfamily Tarsipoidea	110
Superfamily Notoryctoidea	111
Bibliography	112

ABSTRACT

The oldest marsupial fossils have been found in North America and the marsupials are thought to have originated there in the early Cretaceous. The marsupial eutherian ancestor could have had either a marsupial type of viviparity or may have been oviparous. Fossil evidence of early eutherians indicates that the common ancestor may have had a primitive marsupial type of reproduction.

The marsupials are thought to have come to Australia from South America via Antarctica and to have radiated in Australia in isolation, with no eutherian competition.

The Australian radiation was monophyletic and followed three broad lines of evolution: the polyprotodont, didactylous Marsupicarnivora; the polyprotodont, syndactylous Peramelina; the diprotodont; syndactylous Diprotodonta.

INTRODUCTION

An evolutionary study of a group such as the marsupials consists largely of an analysis of their morphological affiliations. Given that the characteristics present in a known organism must have been derived from characters in a more primitive ancestral type, then, when two different known types share the same basic characteristics they are deemed to be related through the common ancestor. Thus, the greater the number of primitive characteristics shared by a group of organisms, the closer we are to being able to describe a hypothetical common ancestor. It follows that the greater the knowledge of morphology of the whole group, then the greater are the chances of deriving an accurate phylogeny within the group.

Included in the Marsupials are numerous extant types and also numerous extinct types which we know from fossils. I agree with Schaffer et al (Schaffer B., M.K. Hecht and N. Eldredge, (1972)) that valid relationships can be inferred using both paleontological and neontological data. Data should not be excluded either on the grounds that it is derived from modern types and therefore lacks historical value (Simpson 1961 p. 83) or that it is derived from fossils and is therefore incomplete. Carefully evaluated data, from whatever field, adds to our knowledge of the group as a whole and therefore should be available for phylogenetic interpretation.

In this thesis, evidence will be drawn from several disciplines. Such evidence should be viewed with regard to the limits of its effective application. I propose first therefore

to briefly discuss the types of data available and to set criteria for their use.

Paleontology

The fossil record is traditionally the starting point for research into the evolution of groups such as the marsupials. In itself, however, a fossil, correctly dated and classified can reveal one absolute fact; that the taxon to which the fossil belongs was living in a known time and place. Analysis of comparative morphology can reveal relationships between different fossils and living animals.

As well as revealing evolutionary trends in the development of a group, the fossil record also provides a time scale against which the evolutionary sequence can be set. This is particularly important in an explanation of the evolution of Australian marsupials where factors such as the invasion of Australia by marsupials and their radiation here in geological isolation requires that a fairly critical time scale be set against evolutionary and geological events.

One of the major problems of paleontology is the selection of morphological characters for comparison. Adaptation is expressed in changes to major functions such as locomotion, feeding, reproduction and perception (Schaffer et al 1972). Fossil skeletal bones provide information on locomotion and feeding. Skulls can provide some information on feeding, sensory apparatus and brain development. Unfortunately, reproductive organs leave little impression on fossil remains.

Added to this is the problem of incompleteness of fossil records. By "completeness" I mean two things, (a) the frequency in geological time with which relevant fossils are found and, (b) the physical state of the fossils themselves. The Australian fossil record has been notoriously poor in the numbers of discovered fossils and there have been no pre-Oligocene marsupial fossils found here. Frequently, when fossils are found they are fragmentary or distorted, often consisting of isolated teeth and jaw fragments which are difficult to interpret. This is hardly surprising when one considers the role of chance in the laying down and subsequent finding of fossil beds (Simpson 1953).

For these reasons much of the analysis of fossil records has been done on teeth and this is valid in so far as teeth do reflect a major function, feeding. However, such studies assume greater validity when they are supported by analysis of other characteristics. This is because the teeth alone, or indeed any other single characteristic could be similar in a number of groups as a result of convergent evolution. It is unlikely, however, that several functionally distinct characteristics would all converge in two or more unrelated groups.

Bearing in mind these limitations and the absence of other data concerning extinct fauna, the fossil record does supply much valuable data for use in evolutionary studies.

Comparative Anatomy and Physiology of Extant Species

In the fossil record it has been observed that sometimes a group of animals has persisted with certain primitive characters whilst related groups have advanced these same characters to a higher level. Amongst the modern mammals some species are considered to be more primitive than others in certain respects. It is possible by anatomical and physiological comparison to derive a sequence amongst recent mammals which suggests an evolutionary sequence. In recent years there has been a renaissance in the study of marsupial anatomy and physiology which has led to an improved understanding of phylogenetic affinities within the marsupials.

Simpson (1961) has stated that such studies are deficient in that lacking the dimension of time, "They are not themselves historical, yet must serve for drawing historical inferences." In fact, difficulties do arise when data based on modern mammals are extrapolated to early evolutionary events. An example of this is the argument concerning the split between the marsupials and the eutherians and the evolution of marsupial reproduction. (Sharman G.B. 1965; Lillegraven Z.A. 1969; Kean R.I. et al 1964).

However, comparative anatomy and physiology of extant marsupials does contribute hugely to the information we have about the shared characteristics of related forms. Taken with the fossil record, evidence from these studies is very useful in understanding phylogenetic affinities within the marsupials.

Serology

One of the most significant recent investigations into the affinities of the marsupials has been the serological research of Kirsch (1968). The study has shown that serological data can be used in the same way as morphological characteristics. In fact Kirsch has contributed an additional characteristic for phylogenetic comparison. The advantage of the study is the extensiveness of its application as it enables comparison of all extant species on the basis of a common complex of characters.

However, Kirsch has shown that sera of some marsupials belonging to different species and even to different families exhibit convergence. He has also shown that all sera have not necessarily evolved at the same rate. This implies that serology should be used in conjunction with data from comparisons of other unrelated characteristics and used in this way it has proved to be a very valuable phylogenetic tool.

Cytology

In the past few years systematists have become increasingly aware of studies in comparative cytology of marsupials. There is more known about karyotypes of marsupials than any other group of mammals. There are several facets of data available from cytogenetic studies. The most fully explored of these are the interspecific comparisons of chromosome number and chromosome morphology.

Sharman (1961) demonstrated the relationships between chromosome numbers and taxonomic groupings. He also showed that problems arise from parallel evolution of chromosome number and

morphology in widely different groups. Comparisons of chromosome arms presented the difficulty of deciding whether the small acrocentric chromosomes actually have arms which should be counted. Hayman and Martin (1965) have suggested that if measurements of chromosome length are corrected for total nuclear D.N.A. content, then a quantitative method of chromosome comparison could be developed. This method is based on the assumption that relative lengths of chromosomes of different species will be in the same ratio as the nuclear D.N.A. content of these species. A corollary of this assumption is that D.N.A. is uniformly distributed along the compacted metaphase chromosomes. So far, cytological studies support these assumptions. The method has been applied successfully to Australian marsupials by Hayman and Martin (1969).

The sex chromosomes of the marsupials have been extensively investigated and interspecific comparisons have been made (Hayman and Martin 1968). Some important observations on phylogenetic trends have been made, but the full significance of these studies is still unknown.

SECTION 1

ORIGIN OF AUSTRALIAN MARSUPIALS

ORIGIN OF MARSUPIALS

Relationships of Marsupials to Other Mammals

Australia is unique in the world in having an extensive marsupial fauna, and a limited radiation of placental mammals. Marsupials are not restricted to Australia however, and there are some sixty endemic species in North and South America. The American marsupials consist of the Didelphidae, and the Caenolestidae. The didelphids are a fairly diverse group containing forms such as the aquatic Chironectes, the vole like, Monodelphis and the arboreal Glenoria. The Caenolestids (seven species) are generalised shrew like marsupials which are now restricted to the Andean temperate rain forests from Venezuela to Southern Chile (Hirshkovitze, 1972).

The origin of marsupials has long been a subject of speculation. In 1880 Huxley divided the mammals into three groups; the Prototheria of which only the monotremes have survived, the Metatheria and the Eutheria. He considered that the Prototheria were ancestral to the Metatheria which in turn gave rise to the Eutheria. This belief stimulated much early work on the anatomy and physiology of the marsupials in the hope that it would enlighten understanding of the evolution of the placental mammals (Mackenzie 1918).

Since then this theory has been discredited. The monotremes have been conclusively ruled out of the marsupial ancestry (Kermack 1963, 1967). It is now thought that the monotremes have been separated from the main line of mammalian evolution since before the development of the theria. Studies of the teeth of the upper Triassic Morganucodon and comparison

with the vestigial dentition of Ornithorynchus imply that monotremes may be related to this early type (Mills 1971).

The marsupials and the eutherians are thought to have shared a common ancestor and an analysis of the features of each group reveals some characteristics held in common, some characteristics unique to each group and others which have evolved convergently in each group. That the marsupials are taxonomically distinct from the eutherians can be shown by a brief summary of their differences. Comparisons of homologous characters are frequently used in forming theories concerning the evolution and origin of each group.

The Brain

In marsupials the structure of the accessory optic tract resembles that of the reptiles and birds, a more primitive condition than that found in the Eutheria. (Lillegraven 1969). The brain of marsupials agrees with the basic structure expected in the Theria, however eutherians possess a corpus callosum which joins and permits the integration of information between the left and right hemispheres. The marsupial brain lacks this but does have a much weaker interhemispherical connection in the form of the anterior commissure in the polyprotodont marsupials. The diprotodont marsupials have the fascius abberans which is a structure functionally analogous to the corpus callosum. It has been suggested that the absence of a corpus callosum in the polyprotodont marsupials is the reason for their somewhat inferior abilities of sensory integration in comparison with placental mammals. (Tyndale-Biscoe 1973, p. 205).

The Skull

Comparisons of the morphology of the tympanic bulla of marsupials and placentals reveals that in the marsupials, the floor of the bulla is covered either partially or completely by a "tympanic wing" of the allisphenoid. This is not seen in eutherians, however the condition seen in didelphoids and certain liptophylous insectivores indicates that a structural ancestor common to both Marsupialia and Insectivora may have occurred soon after the evolution of the mammalian auditory system (Ride 1962). Other features of the auditory system are similar in both marsupials and placentals.

Metabolic Rate

A basic difference between the marsupials and the placentals is the lower metabolic rate of marsupials as measured by O_2 consumption. Dawson and Hulbert (1970) have summarised the metabolic rates of terrestrial vertebrates and have shown that each group of homeotherms has its own characteristic level which is positively associated with body temperature, see Table 1. These differences are thought to indicate that each group acquired a different metabolic level in achieving homeothermy.

Recently, the theory that the development of homeothermy occurred independently in the mammals and birds has been challenged by Bakker (1975). He has argued that homeothermy was achieved in the dinosaur ancestors of the lines leading to the mammals and birds.

Reproduction

The most outstanding differences between marsupials and eutherians are concerned with their modes of reproduction. The marsupials, characteristically, have short gestation followed by the birth of a selectively well developed young with, finding

	Reptiles Lizards	Monotremes	Mammals Marsupials	Eutherians	Birds Non- Passerines	Passerines
Body Temperature °C	30	30	35.5	38	39.5	40.5
Standard Metabolism kJ/kg ^{0.75} /day	31.4	142.3	207.7	288.8	347.4	598.5
Standard Metabolism at 38°C	81.6	259.5	259.5	288.8	301.4	447.1

Table 1. Comparison of Standard Metabolism of terrestrial vertebrates (after Dawson and Hulbert 1970).

its way to the mother's pouch, completes its development attached to one of the teats. In eutherian mammals gestation is long and at birth the infant is comparatively large and generally well developed. When the young marsupial is sufficiently developed to first leave the pouch it approximates the stage of development of the new born placental mammal. Both placentals and marsupials suckle their new born or newly emerged pouch young until weaning is complete.

The arrangements of the urogenital ducts are basic to the differences in reproduction. Understanding of these differences is facilitated by a consideration of development of the urogenital ducts.

In the lower vertebrates, the Wolffian (or Pronephric) ducts grow posteriorly to make contact with the proctodeum and become the main urinary ducts as well as the conveyors of sperm from the testes. The Mullerian ducts grow in association with the Wolffian ducts to become the oviducts. Both ducts, Wolffian and Mullerian, open dorsally into the urogenital sinus. In the mammals a metanephric kidney and ureter develop in the late embryo posterior to the mesonephros as an outgrowth from the Wolffian duct. Subsequently, the Wolffian duct becomes solely a genital duct. The ureter migrates to the ventral part of the urogenital sinus in order to open directly into the bladder.

There are two possible routes which the ureters can take in order to become ventral. Firstly, they can pass between the genital ducts which is the case in the marsupials or, secondly, they can pass outside the genital ducts, which is the case in eutherians. Thus, in the eutherians the Wolffian ducts must loop over the ureters in order to reach the descended testes and the Mullerian ducts are free to fuse in the midline to form a single median vagina. In the marsupials however, fusion of

the Müllerian ducts is impeded by the ureters and the two lateral vaginae must loop around them in order to form the median vaginal sinus. See Fig. 1.

The eggs of marsupials share several characteristics with the monotremes. They are large and surrounded by a shell membrane and a layer of albumen. The outer shell membrane is retained for a large part of gestation in some marsupials. In the placentals, eggs have little or no albumen or yolk and the shell membrane is absent, they are smaller than those of marsupials.

Hormonal control of the estrous cycle is thought to be the same in both marsupials and placentals (Sharman 1965). The major hormonal differences between the two groups becomes apparent during pregnancy. In marsupials gestation cannot endure beyond the end of the secretory phase of the estrous cycle. Intrauterine development of the embryo concentrates on preparing it for the journey to the pouch and survival once there. Therefore the forelimbs and sucking apparatus are well developed. The lungs are partially developed and it is assumed that some respiration takes place across the moist skin. Other functional structures are still very rudimentary.

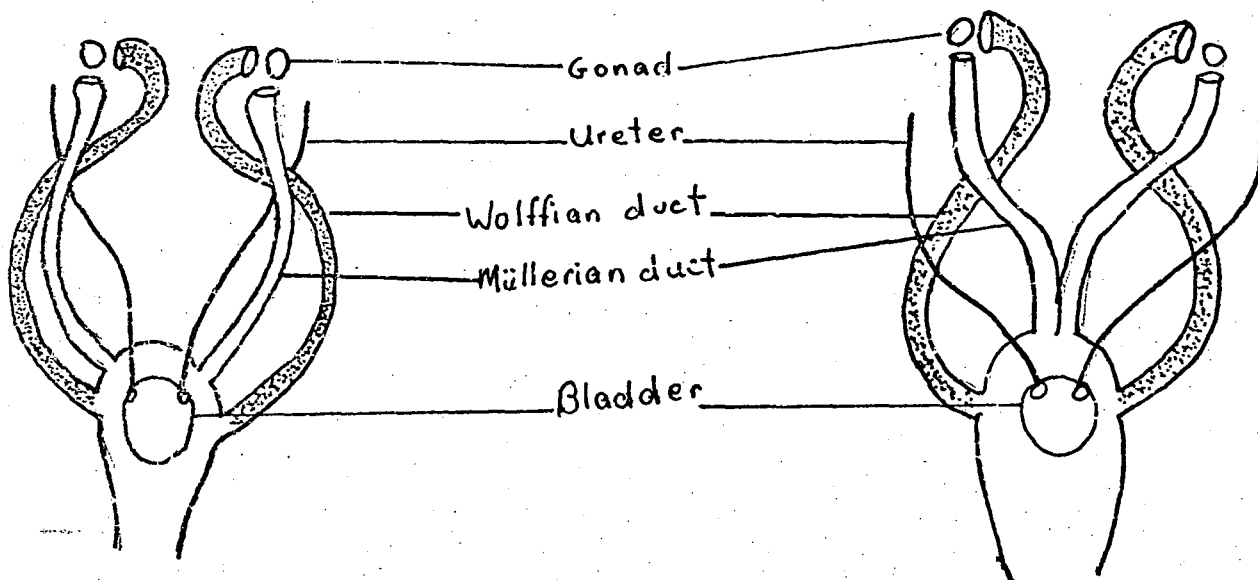
In the placentals gestation is tolerated beyond the limits of an estrous cycle. This occurs because of the secretion of placental hormones, the continuation of progesterone secretion by the corpus luteum and the prolongation of the endometrial secretory phase beyond the non pregnant time of regression. This allows time for the formation of placental membranes and extended intrauterine development of the embryo (see Fig. 2).

At the end of gestation the marsupial embryo is born via the median pseudo-vaginal canal which forms between the median vaginal sinus and urogenital sinus. In some species this

Marsupial

Eutherian

Sexually Indifferent Stage



Adult Stage

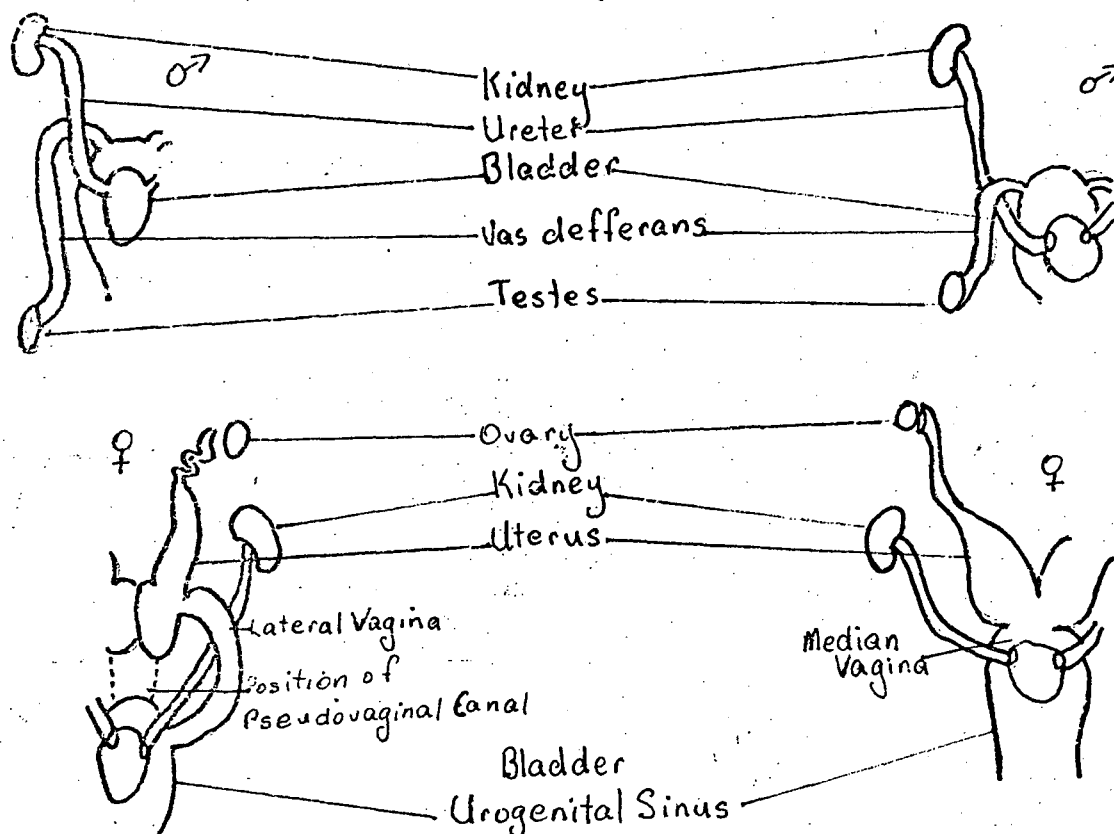


Fig. 1. Development of Reproductive Systems in Marsupials and Eutherians (adapted from Sharman 1965).

canal is formed anew for each parturition, in others it becomes permanent after the first birth. In placentals, birth is by way of the median vagina.

The Pouch

The pouch found in most female marsupials is considered to be homologous to the labia majora of the vulva of eutherian females and equivalent to the male scrotal sac (Lillegraven 1969). The scrotum of male marsupials is anterior to the penis, but with the exception of the lagomorphs is placed posterior to the penis in eutherians.

Epipubic Bones

Most marsupials possess a pair of epipubic bones. They are present in both sexes of all marsupials except for the extinct South American Boryhaenids. It has been suggested by Jellison (1945) that the epipubic bones are homologous with the male baculum and the female os clitoridis of the placentals.

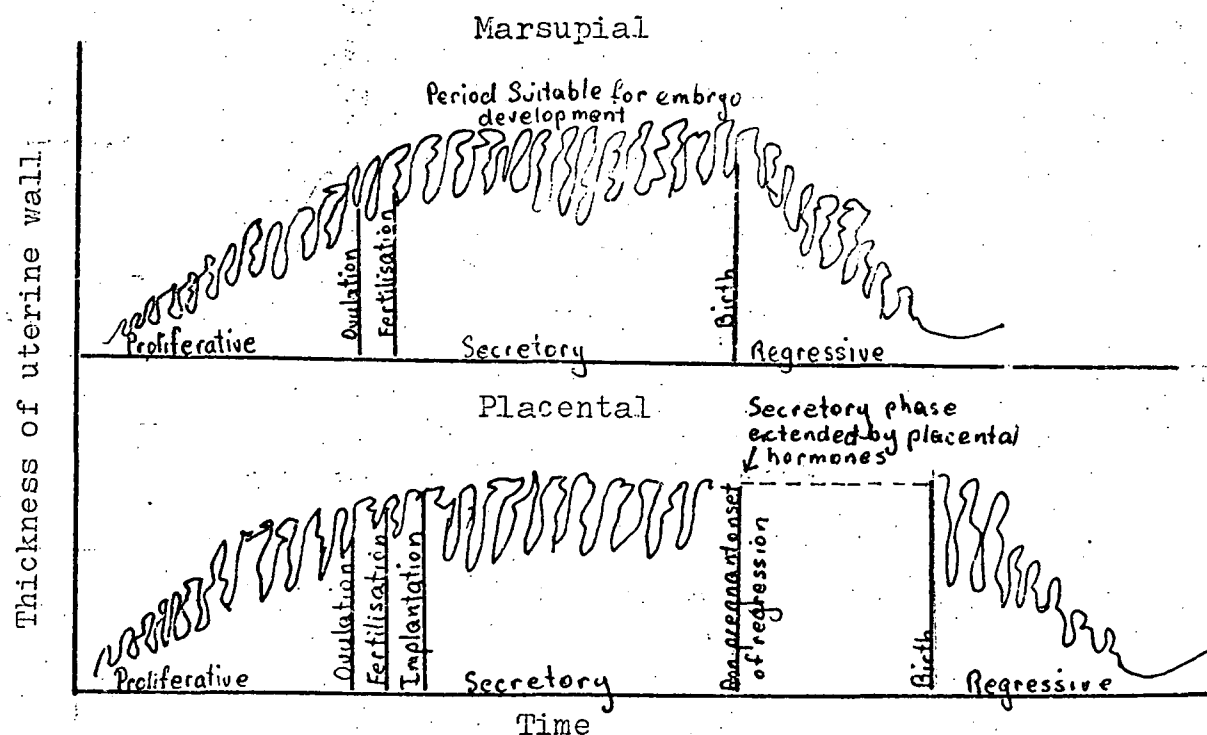


Fig. 2. Hormonal control of estrous cycle and pregnancy in marsupials and placentals.
(After Lillegraven, 1969)

Importance of Dental Characters

In considerations of evolution, great emphasis is always placed on development and modification of various features of dentition. The reason for this is twofold. Firstly, teeth, their number and morphology, reflect evolutionary adaptations made by animals in so far as diet and the acquiring of food are concerned. Secondly, teeth and jaw fragments are the most frequently found fossil fragments.

In the evolution of the Theria one of the most important events has been the development of the tribosphenic type of dentition. This is characterised by upper molars of triangular occlusal outline with a distinct protocone and bipartite lower molars consisting of an anterior section, the trigonid, and a posterior basined heel, the talonid which receives the protocone of the upper molar. See fig. 3.

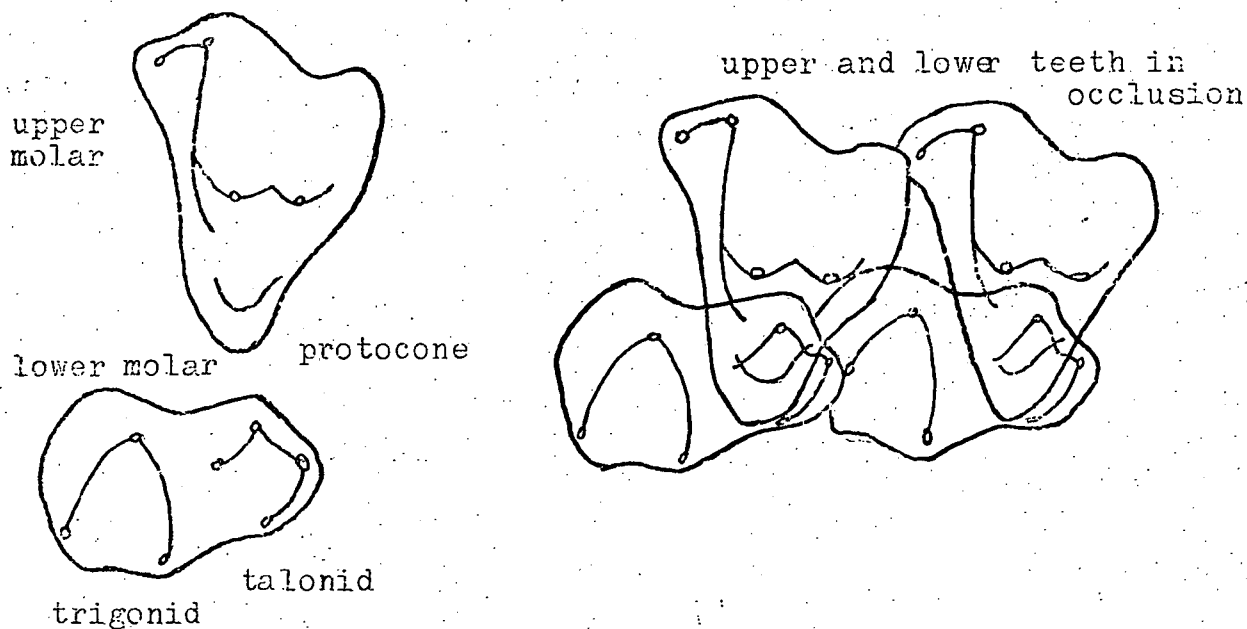


Fig. 3. Tribosphenic dentition found in Pappotherium.
(after Clemens 1968).

The tribosphenic dentition is an adaptation of that found in the Jurassic pantotheres which only permits shearing of food. The tribosphenic dentition permits both shearing and crushing. This combination of characters is advantageous to both omnivorous and predaceous mammals. As both primitive marsupials and eutherians have similar tribosphenic dentition it has been suggested that this dentition was found in the common ancestor. *Aegialodon* from the lower Cretaceous of England has a primitive form of tribosphenic dentition and appears to be a structural intermediate between the molar form found in early mammals such as *Pappotherium* and the eupantotheres such as *Peramus* which lacked tribosphenic dentition (Clemens 1968).

The dental formulae and modes of tooth replacement are also used to taxonomic purpose. The unreduced dental formula of marsupials is four molars, three premolars, one canine and five upper and four lower incisors. Normal tooth replacement only occurs in the most posterior premolar. In eutherians it is three molars, four premolars, one canine and three upper and lower incisors. All of these except the most anterior premolar and the three molars are replaced in the adult (Ziegler 1971).

Evolutionary changes are reflected in changes in dental formula, though Ziegler believes that increase in tooth number does not occur in the antemolar region. Thus modifications to incisor and premolar formulae are reductions, though both increase and reduction has occurred at the posterior end in molar formulae of mammals.

Fossil Evidence

Because the Australian fossil record extends back only as far as the Oligocene (Tedford et al, 1975) it is necessary to look elsewhere for fossil evidence relevant to the origins of marsupials.

The oldest possibly marsupial fossils were found in North America from mid Cretaceous deposits in Texas. Slaughter (1971) has described three important types of the tribosphenic grade of dental evolution from the Butler farm deposits. These are Pappotherium patersoni, Haloclemensia texana, and Kermackia texana.

Haloclemensia texana was identified as a marsupial on the basis of a well developed styler cusp in the 'c' position on the upper molars, incipient twinning of the entoconid and hypoconulid and the increased size of the metacone. Pappotherium patersoni is referred to the eutherian Insectivora because of the presence of a well developed cusp on the metacrista, which does not occur in marsupials, and the indication of a sequence of eruption of permanent premolars from back to front. This sequence of eruption is seen to occur in certain eutherian insectivores.

Kermackia is described as being an intermediate form between types such as Holoclemensia and Pappotherium and a therian known as trinity molar type 6 which appears to be intermediate between certain pantotheres and primitive mammals of metatherian eutherian grade.

Slaughter concludes that these forms show that considerable specialisation in the marsupial and eutherian lines

had taken place by this time in spite of their close proximity to the point of divergence of Metatheria and Eutheria.

The affinity between the earliest marsupials and the insectivores is supported by Ride's (1962) observations on the formation of the tympanic bullae.

It has been pointed out by Clemens (1971) that while Slaughter's conclusion is warranted on the basis of the available evidence, the possibility still remains that the teeth upon which his conclusion is based could have come from animals which were not in the direct line of marsupial or eutherian evolution. It is possible that they formed part of an adaptive radiation of additional types with the tribosphenic grade of dental evolution. See also Turnbull (1971).

Support for Lillegraven's theory has come from Kielan-Jaworowska's (1975) finding that early eutherians from Mongolia show indications of having marsupial epipubic bones. Also studies of the shape of the pelvis in these animals suggests that the neonate was quite small compared with modern eutherians. It seems possible that the early eutherians retained this aspect of marsupial reproduction.

Dental Evidence

Ziegler (1971) proposed a phylogeny of the origin of mammals and the marsupial placental split based on derivations of dental formulae and tooth replacement patterns. This phylogeny is summarised in fig. 4.

Fig. 5. (after ...)

(after ...)

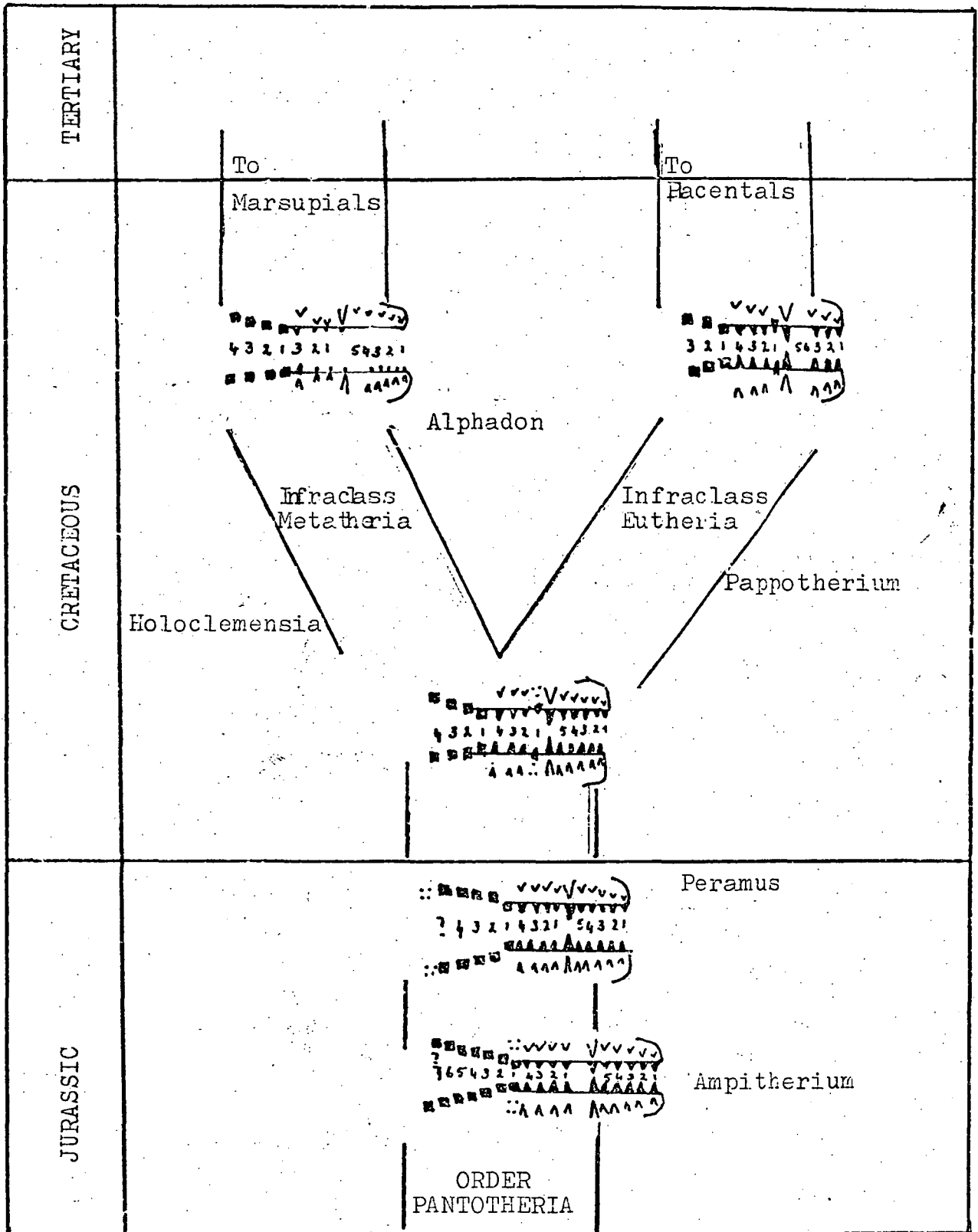


Fig. 4. Diagram of suggested dental formula differentiation in the main line of early Therian evolution (modified after Ziegler, 1971 and Slaughter, 1971).

Reproductive Evidence

On the basis of comparisons of reproduction in extant forms, three conflicting arguments have been put forward concerning the origin of marsupials and the marsupial eutherian dichotomy.

The view that the marsupials evolved from mammals with a eutherian type of reproduction has been proposed by Kean et al (1961). It was suggested that the eutherian median vagina became reduced in the marsupial line as the neonate became smaller. It then followed that the lateral vaginae evolved as seminal ducts.

In a study on reproduction in Trichosurus vulpecula, Kean et al examined the formation of the pseudo-vaginal canal. They found that the formation of the birth canal is commenced early in pregnancy. It is usually unlined but in some individuals it carried a well developed epithelium which was columnar anteriorly, derived from the median vaginal sac, and stratified squamous posteriorly. It is argued that while appearing to organise the formation of the birth canal it forms no protective function (bleeding being controlled by peripheral placement of blood vessels during parturition) and there was no evidence to suggest that it aided parturition in any way.

The lateral vaginae appear to have the same lining and the same derivation as the median canal. The difference is that the lateral canals become clogged during pregnancy.

Kean et al concluded that the presence of epithelial lining of the median vagina is unnecessary and possibly obstructive during parturition. It certainly retards closure

of the canal after birth. Hence it was argued that the epithelial lining is vestigial in the possum rather than rudimentary and the macropods and other marsupials with a permanently lined birth canal illustrate an evolutionary stage which has been almost suppressed in *Trichosurus*.

Embryological evidence for this view is not supportive (Kean 1964).

Lillegraven (1969) has argued that the eutherians could have evolved from a primitive marsupial type of ancestor. Once again arguing from reproductive features, he suggested that the formation of the median vagina in eutherians came about as a result of prolonged gestation and the formation of large embryos. He points out that the eutherian condition could not have evolved until the basic hormonal pathways leading to the extension of gestation had been developed. Since hormonal control of the estrous cycle is essentially the same in marsupials and eutherians, the eutherians could have specialised and developed from this more primitive condition. Once the availability of an extended secretory phase of the estrous cycle had evolved the stage would be set for the early development of placental membranes at the expense of the development of the embryo.

The fundamental difference in the embryological laying down of the urogenital ducts in marsupials and eutherians has been explained earlier in this thesis. Lillegraven considers that this difference is not profound and that the eutherian condition could easily have come about by a unique direction of growth of the uterine bud and by more complete fusion of the Mullerian ducts following selection favouring a muscular, single median birth canal to cope with the birth of a larger neonatus.

Because of the extent of the eutherian radiation which is apparent from fossil records from the late Cretaceous (Lillegraven 1969) he believes that the eutherians must have diverged from the ancestral marsupial stock in the early Cretaceous.

The third argument concerning the origin of marsupial evolution has been raised by Sharman (1970). He has suggested that it is equally probable that marsupials and eutherians have independently evolved viviparity from an oviparous ancestor.

Contrary to Lillegraven's belief that the fundamental differences between the two modes of reproduction are not extreme, Sharman suggests that many features of marsupial reproduction are unique and not directly related to any features found in eutherian reproduction. He cites the formation of the blastocyst during embryological development. This blastocyst is of a type peculiar to marsupials and in certain macropods it undergoes a unique type of embryonic diapause.

Since the chromosomal determination of sex is generally the same in both marsupials and eutherians, Sharman believes that this feature was inherited from the common ancestor.

All mammals exhibit an estrous cycle with a secretory phase. If, as Kermack (1965) has suggested, the monotremes have been separate from Therian line since before the eutherian marsupial split, then the secretory phase is probably a pre-therian development. The secretory phase is not necessarily associated with viviparity since the monotreme egg undergoes a small amount of embryonic development during its passage through the oviduct and absorbs uterine fluid (Hill 1941). Sharman further points out that the hormones estrogen and progesterone

are found throughout the vertebrates though progesterone may function as a hormone only in mammals.

When it is remembered that viviparity occurs in all vertebrate groups except the birds, the possibility of a separate evolution of viviparity in the marsupials appears to be not unlikely on general grounds.

Of the three possibilities, Kean's proposal that the marsupials evolved from a eutherian type ancestor seems the most unlikely. If, those marsupials having a permanently lined median vagina are the most primitive, then we should expect that this structure would be indicated in the embryonic development of the urogenital tract. This is not the case and the median vagina only forms prior to the first parturition by re-organisation of the tissues between the median vaginal sinus and the urogenital sinus.

In the macropods and other marsupials which only bear a single young, the incidence of successful fertilisation, intra-uterine survival and pouch survival are comparatively higher than in eutherians. It appears therefore that the reduction in the number of eggs shed has been accompanied by the development of more efficient methods of intra-uterine care of the embryo and post-natal care of the pouched young (Sharman 1965). The permanently formed pseudo-vaginal canal generally occurs in females of marsupial species which produce only one young at a time. (Sharman 1965, Sharman et al 1966, Tyndale-Biscoe 1965). It seems unlikely that selection would favour the less efficient reproduction seen in dasyurids and didelphids where many young are born and high pouch mortality occurs (Enders 1966).

Of the other two theories, we will probably never know from paleontological evidence exactly what type of reproduction was found in the common ancestor. However, Sharman's proposal does assume a simpler evolutionary process in the derivation of the urogenital tracts of marsupials and eutherians. As the hormonal control of the estrous cycle was probably established in the common ancestor which could have been oviparous, as are the monotremes, then it is simpler to derive the marsupial urogenital tract from the basic reptilian form and similarly the eutherian one, than to firstly evolve the marsupial arrangement and then reverse this arrangement to conform to eutherian requirements.

Paleoecology

During the late Cretaceous the marsupials underwent a wide radiation in North America, with at least thirteen species representing five genera having been found in fossil deposits (Clemens 1968).

It has been suggested (Clemens 1971) that the middle to late Cretaceous was a time of expansion of angiosperm flora with an associated radiation of terrestrial arthropods. Hecht (1969) has noted that an evolutionary radiation of frogs took place coincident with the radiation of angiosperms in the Cretaceous. This would suggest an increase in abundance and diversity of terrestrial invertebrates during this time. Those insectivorous and omnivorous mammals which had the tribosphenic dentition would have been able to take advantage of this expanding food source. The extent of radiation of the marsupials and eutherians

evidenced at the close of the Cretaceous would have taken place largely as a result of the increased availability of a diet suitable to the tribosphenic grade of dentition.

Lillegraven (1969) argues that if the eutherians did evolve from a marsupial type of ancestor, then the dichotomy must have taken place in the early Cretaceous because of the extent of radiation and specialisation achieved by the end of the Cretaceous.

Because of the scarcity of eutherians in the early Cretaceous fossil record of North America, Lillegraven believes that the Eutheria evolved in Asia while the marsupials underwent a separate radiation in North America. In support of this view he points to the fact that once the eutherians do appear in abundance in the fossil record, the marsupials become very scarce. It appears that marsupials do not compete well with placentals and in fact the wide Tertiary South American radiation of marsupials was overwhelmed and displaced by the placentals which invaded the continent during the Pliocene. Thus Lillegraven maintains that the Cretaceous radiation of North American marsupials took place in the absence of eutherians.

Lillegraven argues that the eutherians reached the North American continent towards the end of the Cretaceous. Of the extensive radiation of marsupials which was apparent in the late Cretaceous, only *Alphadon* survived the widespread extinctions which took place at this time.

The Asian fossil beds of the lower Cretaceous have produced one type, *Endotherium*, which has the tribosphenic type of dentition which is thought to have evolved in the ancestors of the Theria. (Kermack Lees and Musset, 1965). More recently,

Butler and Kielan-Jaworowska (1973) have suggested that *Deltatheridium* from the late Cretaceous Djadokhta Formation of Mongolia may in fact be a marsupial. In this case it appears that migration of marsupials from North America to Asia may have taken place.

The Paleocene fauna of North America contains two genera of marsupials, *Peradectes* and *Thylacodon*, both of which are apparently descended from *Alphadon* (Clemens 1968). It is considered (Clemens 1968, Simpson 1945 and others) that *Alphadon* is ancestral to both the South American and Australian radiations.

Whilst Lillegraven and Slaughter agree that the placental marsupial split took place in the early Cretaceous, Slaughter's referral of *Pappotherium patersoni* to the eutheria conflicts with Lillegraven's view that the Eutheria arose in Asia. This discrepancy will not be resolved until more middle Cretaceous deposits containing mammalian fossils are found.

Summary (see Fig. 5)

The marsupials are seen to share certain characteristics with the eutherians. Other features are unique to the marsupials whilst certain other features are seen to be primitive or reptilian.

Fossil evidence indicates an early Cretaceous origin for the marsupials and the eutherians (Slaughter 1971).

Dental evidence suggests that the marsupials and placentals are derived from a pantotherian type of ancestor with a dental formula of five upper and four lower incisors, one canine, four premolars and up to seven molars. This ancestor also

had complete replacement of the incisors, canines and premolars (Ziegler 1971). The common ancestor evolved the tribosphenic type of dentition common to both marsupials and placentals (Clemens, 1968).

Three theories concerning the evolution of marsupial reproduction have been proposed.

Kean (1961, 1964) has suggested that marsupial reproduction is a modification of eutherian reproduction following reduction in the size of the neonate and length of gestation. This theory is not supported by embryological evidence (Kean 1964).

Lillegraven (1969) has argued that the ancestors of the marsupials and eutherians possessed a primitive marsupial type of reproduction. He is supported by recent findings of Kielan-Jaworowska (1975) of the possible presence of epipubic bones in primitive eutherians together with a pelvis of such a shape as to permit the birth of only a very small neonate.

Sharman (1971) suggested that marsupials and eutherians may have evolved their separate reproductive systems from an oviparous ancestor. It is argued that the differences between the two modes of reproduction are profound and Sharman suggests that the hormonal control of the estrous cycle could have been developed in an oviparous ancestor.

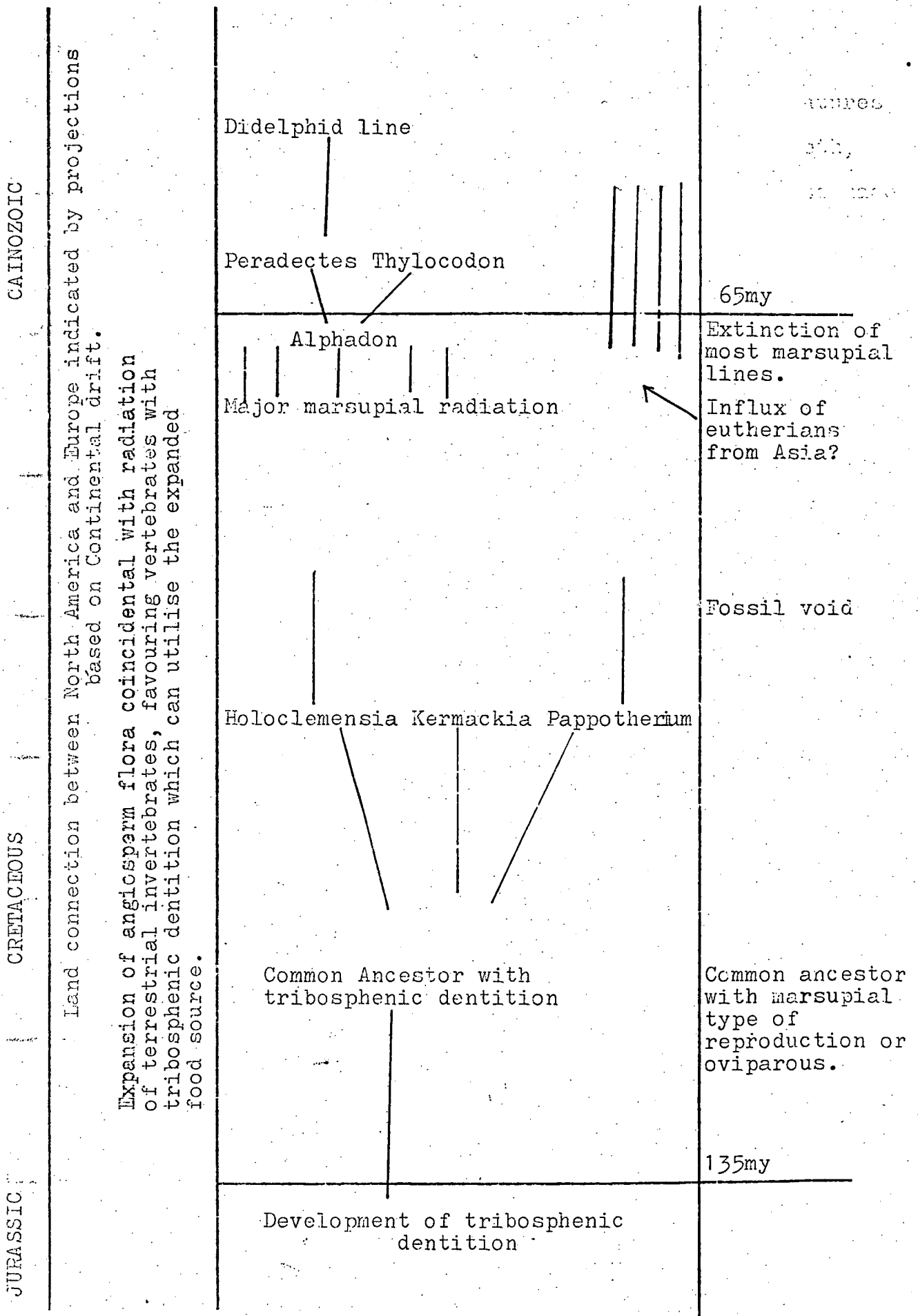
The radiation of marsupials during the late Cretaceous would have been prompted by the expansion of angiosperms at that time which led to an increase in abundance and diversity of terrestrial arthropods. The insectivorous and omnivorous mammals with tribosphenic dentition would have been able to exploit this expanded food source (Clemens 1968, 1971).

Lillegraven (1969) has suggested that the marsupials radiated in isolation in North America and that the placentals developed in Asia. After the placentals reached North America towards the end of the Cretaceous, the marsupials became almost extinct because of their inability to compete with the eutherians.

Of the wide radiation of marsupials in North America, only *Alphadon* survived the extinctions which occurred at the end of the Cretaceous. It is *Alphadon* or a closely related genus which is considered to have been ancestral to the Australian and South American radiations of marsupials (Clemens 1968, Simpson 1945).

Fig. 5.

Summary of Early Marsupial Evolution



DISPERSAL OF MARSUPIALS

South American marsupial fossils first appear in the late Paleocene together with edentales and ungulates. Patterson and Pascual (1972) have reported some teeth from late Cretaceous deposits which appear to be marsupial.

The diversification of Mammals in the late Paleocene suggests that the ancestors actually reached South America somewhat earlier probably in the late Cretaceous or early Paleocene. They appear to be derived from existing North American forms and it has been assumed that they reached South America across a water barrier which excluded other forms contemporaneous with them in North America (Darlington 1957, Patterson and Pascual 1972).

Once established in South America, the marsupials radiated into insectivore, carnivore and to a lesser extent, the rodent adaptive zones. Upper Paleocene deposits have yielded 13 genera of Didelphids, the central stock of the marsupials. The didelphidae are very likely derived from Alphadon of the upper Cretaceous of North America, or some closely related form.

Fig. 6 is a summary of the marsupial radiation in South America.

The carnivorous marsupials have developed widely in the absence of competition from large placental carnivores. The Boryhaenidae paralleled the Australian radiation of the Dasyurids and produced a form, Thylacosmilus which converged the Sabre toothed cats to a remarkable extent. In the Pliocene the Panamanian connection between North and South America was completed. This led to an influx of types from North America, notably the carnivores which Patterson and Pascual consider to

be responsible largely for the extinction of the Eoryhaenidae and also possibly of the more carnivorous didelphids.

Some of the didelphids radiated into North America after the formation of the Panamanian isthmus and today their range extends up to Antarctica.

The South American marsupial fauna is presently restricted to a wide variety of didelphids and small isolated populations of caenolestids (Patterson and Pascual 1972).

The relevance of the South American marsupial radiation to Australia is that it presents a possible pathway from South America to Australia via Antarctica, for the ancestors of the Australian marsupials. Data from studies of Continental drift indicate that Australia was connected to eastern Antarctica until the Eocene (some 50myBb). South America was certainly a part of Gendwanaland and is thought to have separated from West Antarctica as late as the Paleocene (Smith et al 1973). There is no evidence of mammal (apart from bats) colonization of New Zealand until the recent introduction of certain types by man. There was a very wide bird radiation with the flightless Moas occupying to adaptive zones of mammalian browsers elsewhere. The absence of mammals in New Zealand suggests that the marsupials must have reached Australia after New Zealand became separated from Antarctica some 80 million years ago (Rich 1975 p. 66).

If Antarctica was involved in the dispersal of mammals between Southern Continents, then it would need to have been suitably hospitable at the relevant times. Oxygen isotope data reveal that climates at higher latitudes were not severe in the early Tertiary (Keast 1972).

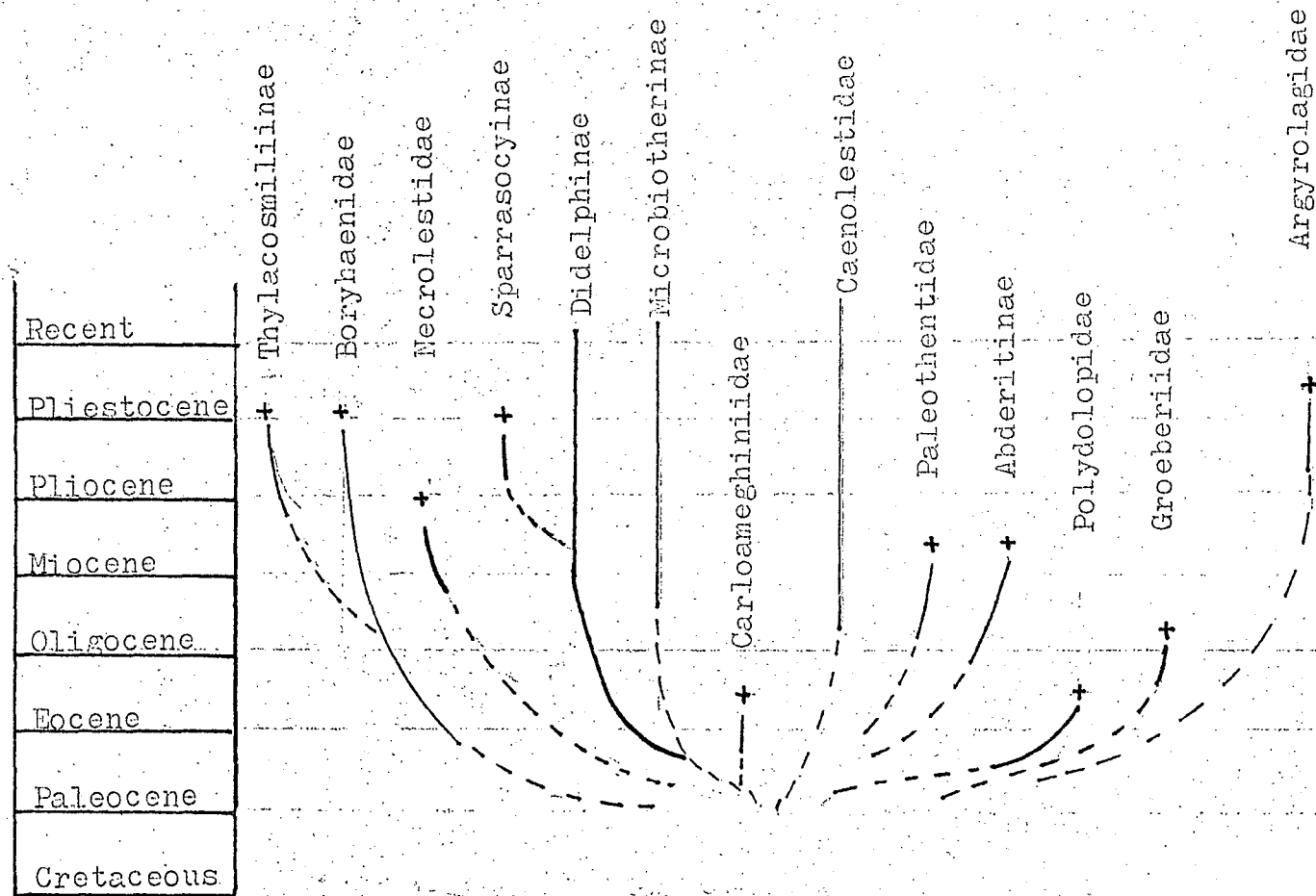


Fig. 6 Summary of the Marsupial Radiation in South America.
 (After Patterson and Pascual, 1972) + indicates extinction.

There is evidence (Margolis and Kennet 1970) that Antarctica was glaciated during the lower Eocene to Oligocene period. The evidence has been questioned by workers such as Fitzpatrick and Summerson (1971). It appears that Antarctica was at least partly vegetated during the early Tertiary (Darlington 1965, Cranwell 1964).

No Tertiary or indeed Cretaceous vertebrate fossils have been found in Antarctica. Triassic deposits have revealed the presence of therapsid reptiles such as *Lystrosaurus* and *Thrinascodon* (Colbert 1971, Elliot et al 1970).

The literature concerning the evidence for an Antarctic dispersal route has been reviewed by Smith (1974), and he has presented a complete bibliography.

If continental drift did occur as recently as is now believed, then the earlier theory (Simpson 1961, Darlington 1957, 1965) of a northern entry of marsupials into Australia from Asia, must be discounted.

SECTION 2

THE AUSTRALIAN RADIATION

THE AUSTRALIAN RADIATION

Classification of Major Groups of Marsupials

Before proceeding with an examination of the phylogeny of the Australian marsupials it is necessary to point out that there is no universally accepted classification.

Simpson (1945, 1970) placed all marsupials in a single order, Marsupialia, within the infraclass Metatheria. He described six superfamilies, three of them American forms and three Australian.

Ride (1964), argued that by analogy with the accepted orders of Eutherian mammals there should be more than one order of marsupials. He proposed four orders within the super order Marsupialia.

Turnbull (1971) accepted Ride's classification but on a higher level he referred the marsupials to the infraclass Eutheria. Thus Turnbull abandoned the use of the name Metatheria (Huxley 1880), by proposing that three cohorts of the Eutheria should be recognised Tribosphenata, Marsupiata and Placentata. Turnbull proposed the cohort Tribosphenata to accommodate the Trinity Therians which he believes to be of a grade which cannot be described as either Marsupial or Placental.

Kirsch (1968a, 1975) has proposed a classification based largely on the results of serological studies, he has divided super order Marsupialia into three orders which are synonymous with Ride's orders except for the fact that Ride's Order Peramelina is included in the order Polyprotodonta as super family Peramelemorphia. The implications of this difference are important and will be discussed in a later section.

A summary of the major classifications still in use is given in Table 2.

Table 2.

Turnbull (1971)

Sb.C. Prototheria
Sb.C. Theria
In.C. Eutheria
Co. Tribosphenata
Co. Marsupialia
O. Marsupicarnivora
O. Peramelina
O. Paucituberculata
O. Diprotodonta
Co. Placentata

Kirsch (1968)

Sp.O. Marsupialia
O. Polyprotodonta
Sb.O. Didelphimorphia
Sb.O. Dasyuromorphia
Sb.O. Peramelemorphia
O. Paucituberculata
Sp.F. Caenolestoidae
O. Diprotodonta
Sp.F. Vombatoidae
Sp.F. Phalangeroidae
Sp.F. Tarsipedoidae

Ride (1964)

Sp.O. Marsupialia
O. Marsupicarnivora
O. Peramelina
O. Diprotodonta

Simpson (1945, 1970)

O. Marsupialia
Sp.F. Didelphoidea
Sp.F. Dasyuroidea
Sp.F. Perameloidea
Sp.F. Phalangeroidae
Sp.F. Argylorhagoidea

For the remainder of this thesis I intend to use the simpler classification of Ride (1964) with reference to that of Kirsch where differences occur.

It is interesting to note here that both Kirsch and Ride have ignored Simpson's (1972) alternative classification where the American and Australian marsupials have been placed into separate groups. This is despite Kirsch's serological evidence that all Australian types are more closely related to each other than to any American forms.

Evolution of Marsupials within Australia

Serological Studies (Kirsch 1968⁹⁵) have revealed that the Australian marsupials are more closely related to each other than to any extant American forms. This indicates that the Australian radiation is monophyletic. The view that the Australian marsupials were derived from a didelphoid radicle composed of animals with dentition similar to Alphadon has been supported by Clemens (1968, 1971), Van Valen (1969), Simpson (1948, 1971) and Ride (1964).

Simpson (1971, p. 43) has stated that the primitive didelphids and the primitive dasyurids were probably barely or not distinguishable. The didelphids formed the nucleus of the South American radiation and the dasyurids were ancestral to all Australian forms.

The Australian radiation did not necessarily take place entirely within Australia. If the Marsupials did reach Australia via migration route such as Antarctica, then it is to be expected that various evolutionary adaptations should have taken place during dispersal. Thus it is possible that a diversity of forms entered Australia.

Australian marsupials fall into three structural groups: -

- (a) polyprotodont and didactylous,
- (b) polyprotodont and syndactylous, and,
- (c) diprotodont and syndactylous.

The above grouping of the marsupials largely forms the basis of Ride's (1964) classification.

The first group of polyprotodont, didactylous marsupials are represented in Australia by the dasyurids and the thylacinids. These are included in the order Marsupicarnivora.

The order Peramelina consists of all the marsupials exhibiting polyprotodonty and syndactyly. These are the bandicoots, a small group with approximately twenty species. Kirsch (1968(b)) has placed the peramelids together with the dasyurids in his Order Polyprotodonta. This is because his serological data showed the peramelids to be more similar to the dasyurids than to the phalangerids. Ride (1968) however preferred to regard the serological similarity as a case of conservatism in serological characters.

The third structural group of marsupials which are diprotodont and syndactylous constitute the Order Diprotodonta. The phalangerids, macropodids and the vombatids belong to this order together with the extinct Wynyardia and diprotodontids. As well as being diprotodont and syndactylous the members of this order also possess a fasciculus abherans in the forebrain (a condition known as duplicommissuraly). (Abbie 1941) (see Section 1).

Ride's phylogeny showing relationships of the Australian marsupial orders is based on his conclusion that the structural groups represent a developmental series. See Fig. 7 .

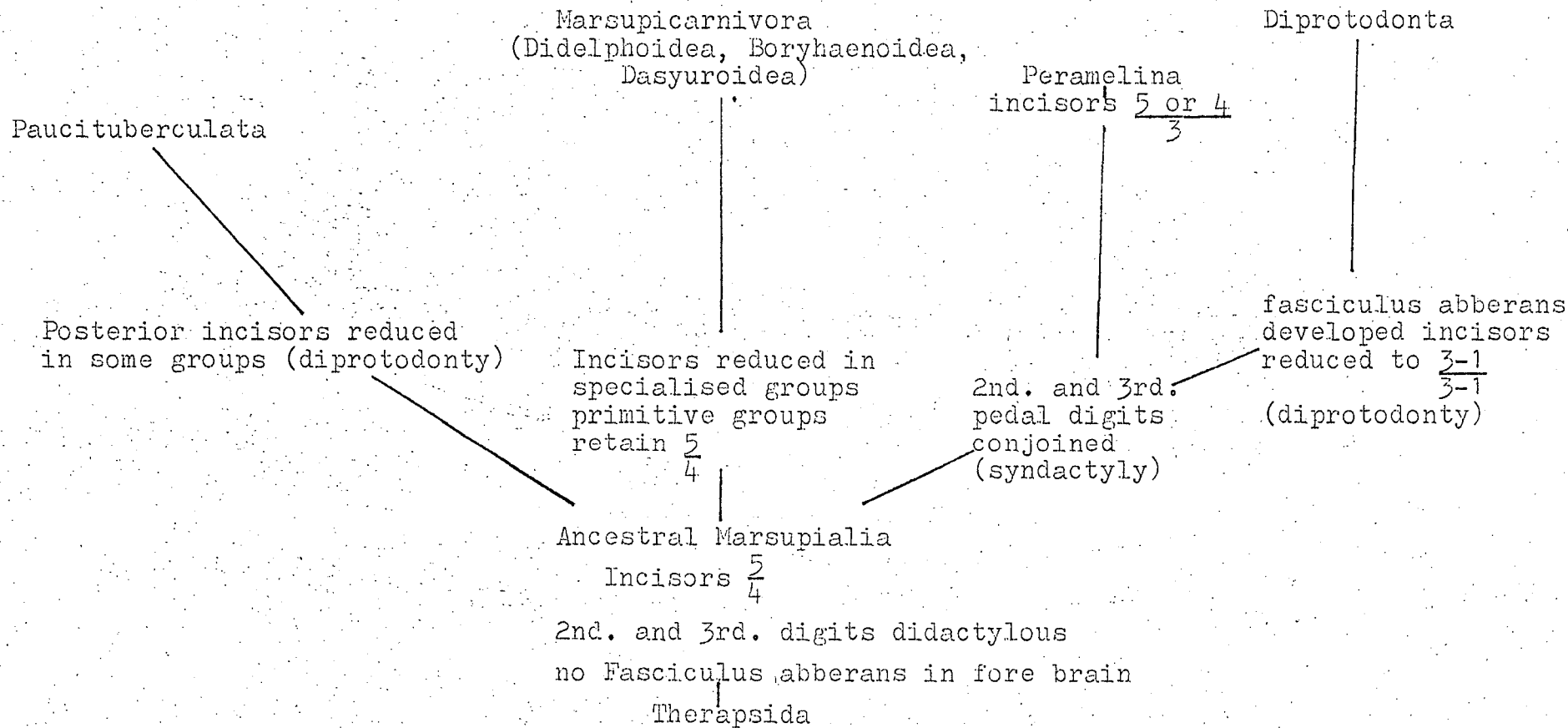


Fig. 7. Phylogeny of Orders of Marsupials (after Ride 1964).

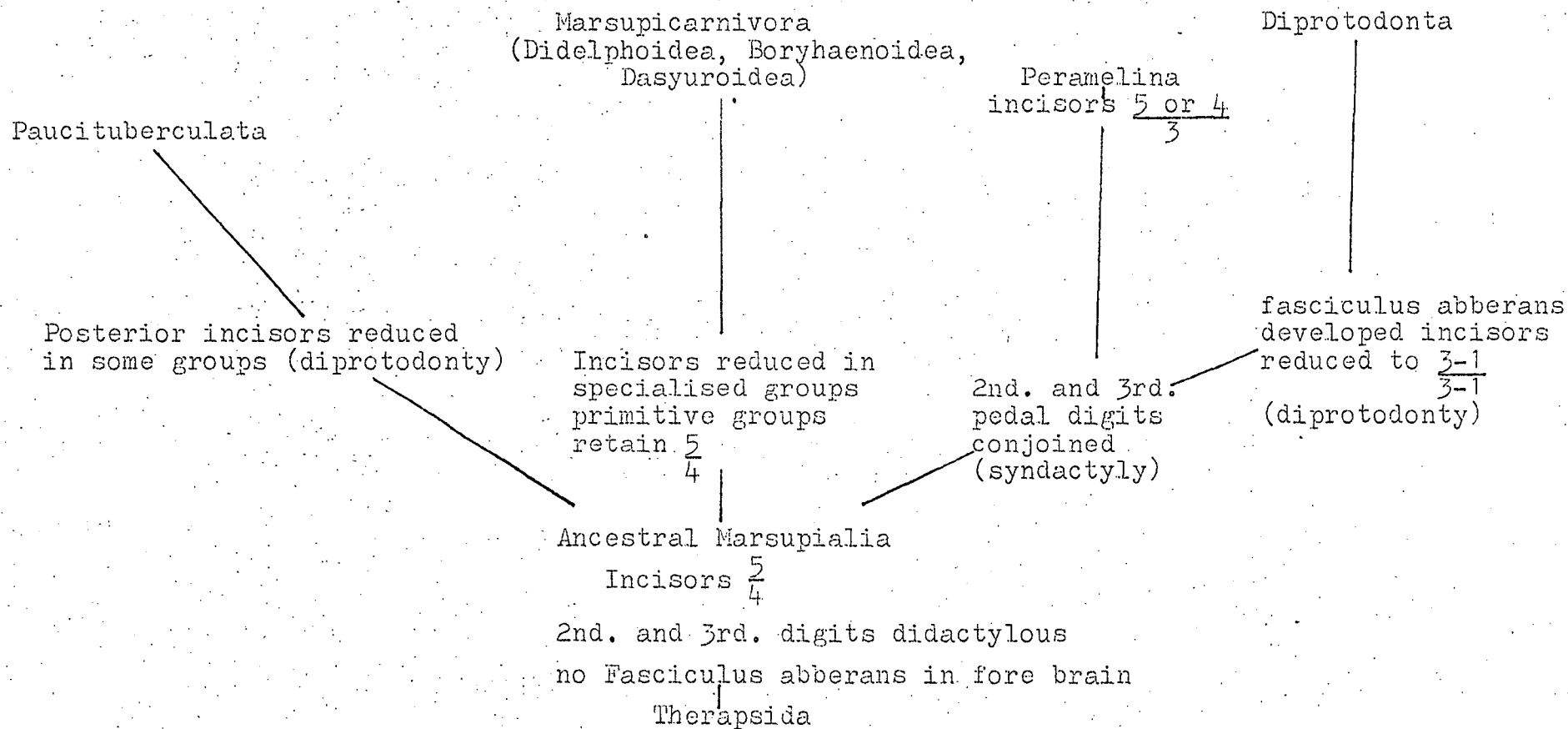


Fig. 7. Phylogeny of Orders of Marsupials (after Ride 1964).

In this phylogeny, Ride assumes that syndactyly arose only once, in the line leading to the perameloids and to the Dipratodonta. As previously stated, Kirsch (1968) found the peramelids to be serologically closer to the dasyuroids than the phalangeroids. This suggests that those two groups could have evolved from the same stock from which the diprotodont line had already split. If this is the case, then syndactyly must have evolved twice. Simpson (1970) in considering the question of the evolution of syndactyly, pointed out that the condition has arisen quite independantly in Potamogale (a placental). However, he concludes that the question 'of possible independant origin of syndactyly in Perameloida and Phalangeroida must thus still be considered open...".

More recently, support for a single origin of syndactyly has come from Marshall (1972). From studies of foot structure he concluded the foot structure of the dasyurids may have been the condition found in the ancestors of all Australian marsupials. Phalangerid syndactyly is clearly derived from the dasyurid condition and probably forms the line from which branched the peramelid and macrapod lines.

There is no fossil data concerning the ordinal evolution of the Australian marsupials.

Chromosomal studies reveal that in all species so far studied, the dasyurids have chromosome number of $2n=14$ with similar chromosome morphology. Myrmecobius exhibits a dasyurid type of chromosome complement (Sharman, 1974). Thus the dasyuroids form a discrete group on the basis of chromosome number and morphology.

The Peramelinae has chromosomes like the dasyurids except that the X and Y chromosomes are much larger. However, Sharman (1961, 1974) considers that this does not imply a close relationship or the sharing of a primitive karyotype. In the other peramelid subfamily, the Thylacomyinae, a multiple sex chromosome mechanism resulting from fusion of X chromosomes on to a pair of autosomes has caused a reduction of the chromosome number from $2n=20$ to $2n=18$ (Sharman 1974). Since the Peramelinae and the Thylacomyinae must have evolved from a common ancestor, then it seems likely that the chromosome numbers of $2n=14$ and $2n=13$, 19 were derived from an ancestor with a higher chromosome number. Hayman and Martin (1967) have suggested that the $2n=14$ forms could have been derived from a $2n=20$ form by Robertsonian fusions.

In the order Diprotodonta the chromosome number varies from $2n=10$ to $2n=32$ (Hayman and Martin 1969).

The super family Phalangerida has three families and of these, the Burramyidae all have chromosome number $2n=14$. As with the Peramelidae Sharman (1974) points out that no close relationship with Dasyuridae can be inferred from this. In the Phalangeridae and Petauridae it is observed that chromosome number $2n=20$ is most frequently found. (See Table 3).

In the Macropodidae the most common chromosome number is $2n=22$. However, species of the genus *Dendrolagus* have chromosome number $2n=14$ and in *Macropus* $2n=16$.

The grouping of genera of marsupials is summarised in Table 3.

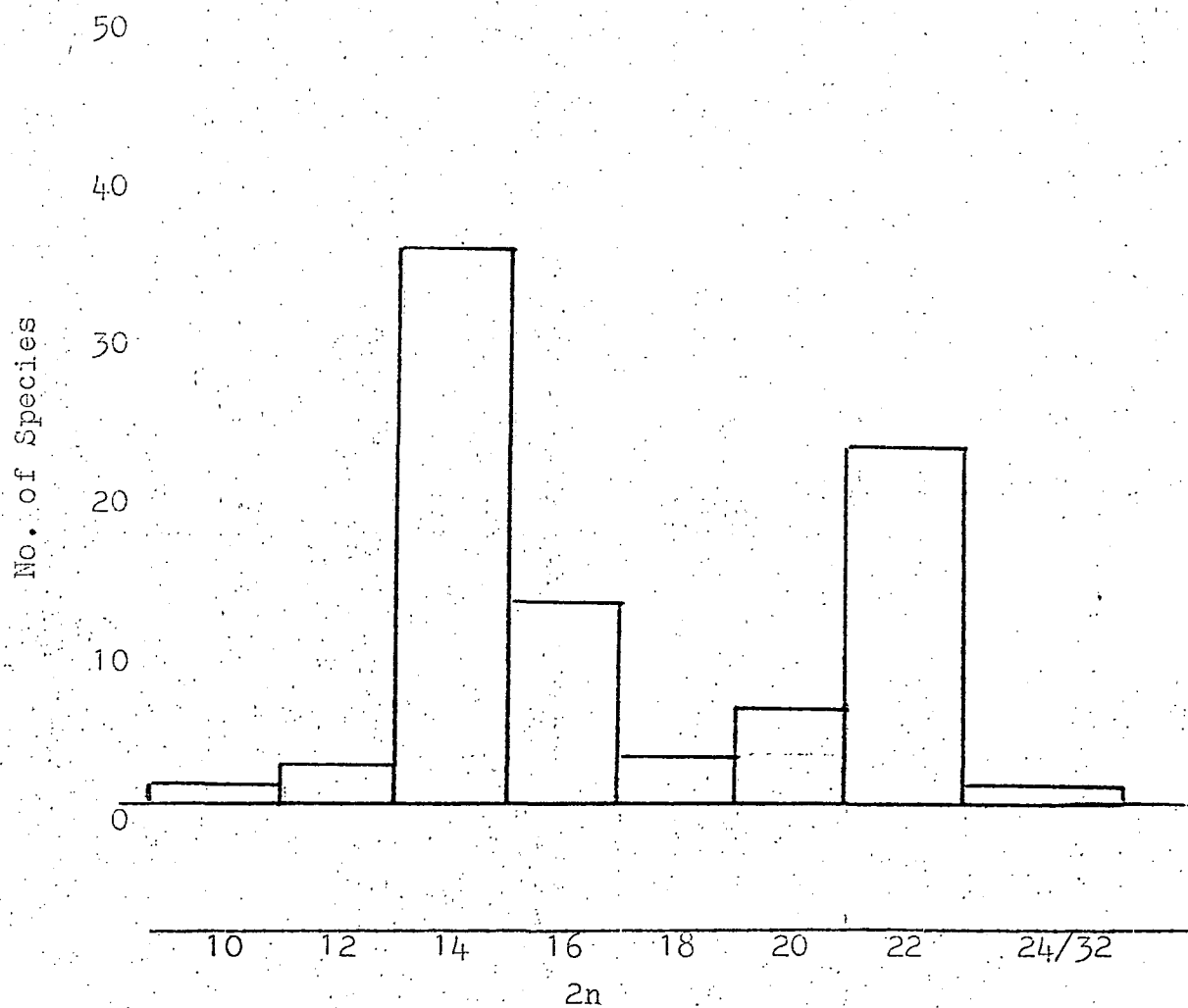
Table 3. Grouping of Genera of Marsupials According to Chromosome Number.

	20 or over	14	Intermediate
Didelphoidea Didelphidae	3 genera 4 species	3 genera 3 species	
Caenolestoidea Caenolestidae		2 genera 2 species	
Dasyuroidea Dasyuridae		8 genera 13 species	
Perameloidea Peramelidae		2 genera 5 species	
Thylacomidae			1 genus 1 species
Vombatoidea Vombatidae		2 genera 2 species	
Phascolarctidae			1 genus 1 species
Phalangeroidea Phalangeridae	2 genera 3 species	1 genus 1 species	
Petauridae	4 genera 4 species		1 genus 1 species
Burramyidae		3 genera 5 species	
Macropodidae	11 genera 18 species	2 genera 5 species	3 genera 13 species
Tarsipedoidea	1 genus 1 species		
Notoryctoidea	1 genus 1 species		

Modified from Hayman and Martin 1969 (additional data from Hayman, Kirsch, Martin and Waller 1971, Yunis, Cayon and Ramirez; 1972, Calaby, Corbet, Sharman and Johnston 1974).

When a histogram of the distribution of chromosome numbers in marsupials is plotted (Fig. 8), a bimodal distribution around 14 and 22 is observed.

Fig. 8. Distribution of Chromosome Numbers in Marsupials.



Modified after Sharman (1973)

The question arises as to which is the primitive marsupial karyotype. Sharman (1973, 1974) has pointed out that there are only three marsupials with more than 22 chromosomes and that there is good evidence of evolutionary lowering of chromosome number. Also, the independent evolution, a $2n=14$ karyotype appears to have occurred in several marsupial groups. He concludes that while $2n=14$ may be the primitive karyotype, it is possible that it is derived from the $2n=22$ karyotype.

Hayman and Martin (1969) favour the interpretation that the Australian species were derived from a $2n=14$ stock with subsequent and independent evolution of $2n=22$ in some groups. (Hayman, et al 1971) believes that the similarities between the Chromosome complement of the South American Caenolestids and the Australian Dasyurids, both $2n=14$ and with similar morphology, "confirms the hypothesis that $2n=14$ with this form of complement is ancestral for the marsupials."

Conclusion

The Australian marsupials represent a monophyletic radiation, from a primitive dasyuroid-didelphoid ancestor. The radiation involved the evolution of three structural groups; the polyprotodont, didactylous dasyuroids (order Marsupicarnora), the polyprotodont, syndactylous Peramelina and the diprotodont, syndactylous Diprotodonta. Whether the Peramelina and the Diprotodonta arose from a single syndactylous ancestor is still unresolved although study of the anatomy of marsupial feet (Bensley 1903, Marshall 1972) suggests that this was the case.

Chromosomal studies indicate that the Australian radiation arose from a dasyurid ancestor with a primitive karyotype and chromosome number $2n=14$.

SUPERFAMILY DASYUROIDEA

Bensley (1903) pointed out that the Dasyuroidea are distinguished from other Australian marsupials in that they represent a line of evolution involving progressive changes from a primitive insectivorous type indicated in the dentition of the smaller dasyurids to the specialised carnivorous forms such as *Sarcophilus*. He included *Thylacinus* and *Myrmecobius* in the family Dasyuridae but stressed that they could have developed separately. He divided the Dasyuridae into three sub-families, Dasyurinae, Thylacininae and Myrmecobiinae.

Since Bensley's classification, the Thylacines, *Myrmecobius* and the marsupial mole *Notoryctes* have remained controversial with regard to their affinities with the dasyurids.

Wood (1924) compared forty-nine anatomical characters of *Thylacinus* with the extinct South American *Boryhaenidae* and *Didelphidae*. He concluded that the boryhaenids were specifically related to the Thylacines as opposed to the other South American forms and the Australian Dasyuridae.

This conclusion was challenged by Simpson (1941) who pointed out that Wood's comparisons showed mainly that the three types shared a common ancestor as did the dasyurids. He remarked that the evidence showed fairly conclusively that *Thylacinus* was merely a specialised dasyurid.

Tate (1947) regarded Bensley's classification as extreme and pointed out the similarities between the dentition of *Thylacinus* with an unreduced P_4^4 and the then newly discovered *Murexia*. He confined *Thylacinus* to the status of a genus.

In 1964 Ride proposed that *Thylacinus* should be raised to the level of a family, Thylacinidae, within the

superfamily Dasyuroidea. Ride concluded that Notoryctes, whilst warranting family status could not be confidently placed into an order.

Thylacinidae and Notoryctidae are recognised as families in all recent classifications whilst Mynmecobius is afforded family status by Kirsch (1975) and sub-family status by Ride (1964).

Family Dasyuridae

Modern dasyurids exhibit all grades of carnivorous specialisations from insectivorous - small vertebrate eating forms such as Planigale and Sminthopsis to the specialised mammal killers and carrion feeders such as Sarcophilus. This gradation of carnivorous development through the family generally occurs without reference to generic distinction and is closely related to increase in body size (Bensley 1903).

The fossil record of Dasyuridae is poor and mainly restricted to the larger forms. In general considerations of evolution it is of little use and the phylogeny of the group has been mainly derived from neontological studies.

Studies of dentition in living Dasyurids reveals that the ancestral form probably possessed the dental formula $\frac{4134}{3134}$ which is deriveable from the largest formula known for marsupials $\frac{5134}{4134}$ which occurred in fossil didelphoids. (Simpson 1941). Van Valen (1969) argued that the primitive dasyurid type of carnassiality is deriveable from that found in Alphadon which shows a relatively low grade of carnassial specialisation.

Tate (1947) has listed other characters which he ascribed to the ancestral dasyurid and incidentally the ancestor of all Australian Marsupials. These are as follows: small,

about rat sized; skull long faced with slight post orbital eminences, slightly constricted mid-brain area, unreduced hind brain area; bullae small, more or less hemispherical; periotic slightly inflated; paraoccipital processes free from inflated area; pterygoids falcate; palate with short anterior foramina and small or perhaps no posterior openings; i^1 specialised, late in erupting and set off from i^{2-4} by a diastema, i^4 larger than i^2 ; $p^{1,3,4}$ each successively larger than the preceding tooth with simple sub-triangular cusps; mp_4^4 molariform, not extremely small; m^{1-3} with complete tritubercular set of cusps and styles; m^4 reduced to accommodate its terminal position in the tooth row; i_{1-3}^1 semi-recumbent with i_1 the largest of the three; p_4 slightly smaller than p_3 ; feet with striated pads; number of toes unreduced; third anterior digit slightly dominant; 2nd and 3rd digits not joined in pes, didactly; tail about as long as head and body, not capable of incrassation; pouch probably complete and backwards opening; number of nipples ranging from eight to ten. Ride (1964) has raised the point that in the dasyurids, the epitympanic sinus is always enclosed ventrally in an alisphenoid bulla which grips the tympanic ring laterally. It is widely open into the epitympanic recess posteriorly. The dorsal and anterolateral part of the epitympanic sinus is also greatly excavated into the alisphenoid and squamosal and may even penetrate into the root of the zygomatic arch dorsal to the glenoid. This situation seems to be more specialised than that of *Didelphis* where there is no dorsal or anterolateral excavation and the cavity is only partly floored by a tympanic wing of the alisphenoid.

It is possible therefore, that the ancestral dasyurid had developed the tympanic wing of the alisphenoid beyond the

condition found in the early didelphoids.

Tate (1947) defined two main lines of dasyurid evolution. In the least specialised line p_4^4 is either retained or found only slightly reduced in the milk premolars. (See also Bensley 1903). This group he called the Phascogalinae and the most primitive member is Murexia. (Tate referred Thylacinus to this group).

Members of this group, Sminthopsis, Antechinus, Planigale and Phascogale all exhibit a scampering type of locomotion; unreduced digital formulae unmodified claws, pads with primitive striations and an unmodified tail. Tate considered features such as modifications of the ear pinna and of the pouch and mammary to be recent adaptations as opposed to ancient characteristics.

Murexia is distinguished from Antechinus, Sminthopsis and Planigale by narrowing of the nasals in the case of Sminthopsis and the reversal of the incisive gradient in the case of Planigale and Phascogale. Planigale shows a slight reversal of incisive gradient which becomes marked in the Phascogale. Thus the trend over this group is for i^2 to become larger than i^4 .

Generally, the interorbital region in the Antechinus group is broad whilst it is narrow in the more typical members of the group. In Antechinus the postorbital processes are absent; the size of the auditory bulla is small to medium, hemispherical in form and the pads of the feet are usually striated.

The other evolutionary line described by Tate is the Dasyurinae where p_4^4 are either absent or reduced. In Neophascogale there are no post orbital processes, the mid-brain is narrowed and the fore-brain region is not unduly broadened. In Phascolosorex and Myotis the post orbital processes are incipient. The

members of *Dasyurus* have constricted mid-brain regions and broadened fore-brain regions. The post-orbital processes are incipient or well developed. *Dasycercus* has a similar intertemporal condition to *Dasyurus*. In *Sarcophilus* the broadening of the olfactory fore-brain area is greatly increased and the post-orbital processes enclose a substantial segment of the orbit. *Dasyuroides* has neither intertemporal constriction of the mid-brain nor development of post orbital processes.

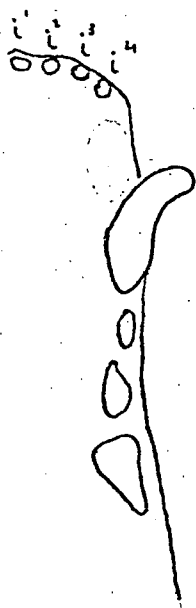
Comparisons of Dental Characters within the Dasyuridae

There are two types of upper incisors in the Dasyuridae; i^1 narrow, pointed and more or less proodont, with delayed eruption relative to i^{2-4} ; i^{2-4} generalised cutting incisors, broad, bladelike and erupting earlier than i^1 . i^1 is usually set apart somewhat from i^{2-4} . Thus i^1 and i^{2-4} are distinguishable by shape, size (i^1 larger than i^{2-4}), function and development (Tate 1947).

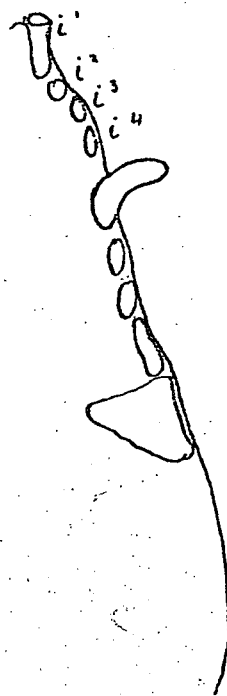
The trend in the dasyurids is towards normalisation of i^1 relative to i^{2-4} with the incisor row tending to become transverse to the premolar rows (*Sarcophilus*, Dasyurinae) rather than parallel to them (*Neophascogale*) (See Fig. 9).

Eruption of i^1 is still delayed however in forms where it is undifferentiated from i^{2-4} .

In *Antechinus* and *Phascogale* i_2^2 are larger than i_{3-4}^{3-4} . In *Neophascogale*, *Phascolorex*, *Myoctis*, *Dasyuroides*, *Dasycercus*, *Dasyurus* and *Sarcophilus* i_2^2 are smaller than i_4^4 (Tate 1947).



D. maculatus



Neophascogale

Fig. 9 Comparison of incisor rows in Dasyurinae and Neophascogale (Jones 1925).

Premolars.

The Dasyuridae exhibits a trend towards obsolescence of P_4^+ . Reduction to some degree of P_4^+ is seen in all dasyurids except Murexia and Sminthopsis rufigenis (Bensley 1903).

Molars (Bensley 1903)

The molar pattern in the small dasyurids is similar in most species. The upper molars are trituberculate in the manner of those found in most insectivorous mammals. The three cusps, protocone, metacone and paracone are of a piercing shape and the paracone is small in comparison with the other two cusps.

The metacone is the dominant cusp and its posterior border is modified to form a trenchant spur which shears against the antero-external border of the triangular pillar of the succeeding lower tooth.

The lower molars have a short and broad crown of tuberculo-sectorial pattern being composed of an anterior triangular trigonid with posterior heel, the talonid. The trigonid has three cusps of which the protoconid is most developed while the metaconid is smaller and the paraconid still more so. The antero-external side of the trigonid formed by the paraconid and protoconid is trenchant and shears against the metacone-spur of the preceding upper molar. There is also a small antero-external shelf on the trigonid. The talonid is basin shaped and its edge has two inner and one outer cusps representing the entoconid which is vestigial, the hypoconulid and the hypoconid.

In the larger members of the *Dasyuridae*, with increased carnassiality the upper molars are modified in the following ways; reduction of the protocone; enlargement of the metacone with lateral compression at its tip to form a trenchant blade and encroachment of its base on the protocone root; elongation of the trenchant metacone spur and rotation inwards of its distal end so that it shears inwards rather than backwards; lateral compression of the teeth so that the external styles become approximated to their respective cusps.

In the lower molars the carnivorous modifications include: enlargement and lateral compression of the trigonid; conversion of the tips of the paraconid and protoconid into trenchant blades; outwards rotation of the shearing edge formed by the adjacent edges of the protoconid and paraconid; reduction of the metaconid; reduction of the talonid.

The dasyurids all have the same chromosome number $2n=14$, and the morphology of their chromosomes is similar with *Sarcophilus* showing the greatest deviation from the "standard dasyurid" karyotype (Martin and Hayman 1967).

Tate (1947) derived a phylogeny of the dasyurids based on comparisons of modern forms. (Fig. 10)

The oldest known fossil dasyurid is from the late Oligocene Ngapakaldi formation of Central Australia (Stirton et al 1961). Stirton et al suggested that the fossil possibly represented a stage in the evolution of *Thylacinus* because of the possession of three premolars graded from front to rear, and the lack of a metaconid on M_1 . Ride (1964) however, has pointed out that some dasyurids such as *Antechinus rosamondae* exhibit a much reduced metaconid on M_1 . Other dasyurids such as *Sminthopsis* and *Murexia* possess three premolars which increase in size from front to rear. Ride believes this fossil to be a possible ancestral dasyurine.

Stirton et al (1968) have recorded an undescribed dasyurid from the Miocene Kitjamarpu fauna of South Australia.

Dasyurinae dunmalli from the Pliocene Chinchilla sands fauna (Bartholomai 1971), is similar to *D. viverrinus* except that it possesses a minute third premolar.

A very important fossil in considerations of the evolution of *Sarcophilus* and its affinity with the Dasyurinae, is *Glaucodon ballaratensis* (Stirton 1957). As previously mentioned, there is a trend in the Dasyuridae towards increased carnassiality with shortening of the face expressed in the direction of the incisor row. *Sarcophilus* differs from the large Dasyurinae in having a shorter face and a more transverse incisor row. In *Sarcophilus* emphasis has been placed on development of the

paraconid crest especially between the paraconid and the protoconid. The talonid and metaconid are reduced in comparison with the primitive dasyurid type. Ride (1964) compared the dental features of *Glaucodon* with those of *Sarcophilus* and *D. maculatus*. (Table 4). He concluded that with regard to these features, *Glaucodon* could be regarded as being structurally ancestral to *Sarcophilus* whilst still retaining some dasyurine features. In one feature, the well developed conical but adpressed metaconid on M_1 , it resembles neither of these two groups.

	D. maculatus		Glaucodon	Sarcophilus	
	n	Range %	%	Range %	n
1. Total length of M_{1-4} as % of length of mandible from tip of posterior edge of masseteric shelf	3	29.8-33.2	39.6	37.8-42.7	7
2. Length of M_4 excluding talonid as % of total length of M_4 .	5	67.7-77.1	77.0	92.0-97.4	8
3. M_4 height of paraconid as % of protoconid	5	52.6-63.3	56.1	63.4-72.2	6
4. M_4 height of metaconid as % of protoconid	5	52.6-60.7	42.7	31.3-38.0	6
5. Depth of mandible as % of length of mandible from anterior tip to posterior edge of masseteric shelf	4	15.7-16.7	20.5	21.7-23.0	7
6. Depth of mandible as % of molar tooth row	3	49.8-56.2	51.9	51.5-58.9	7

Table. 4 Comparison of Characters of *Dasyurus maculatus*, *Glaucodon* and *Sarcophilus*. (After Ride 1964).

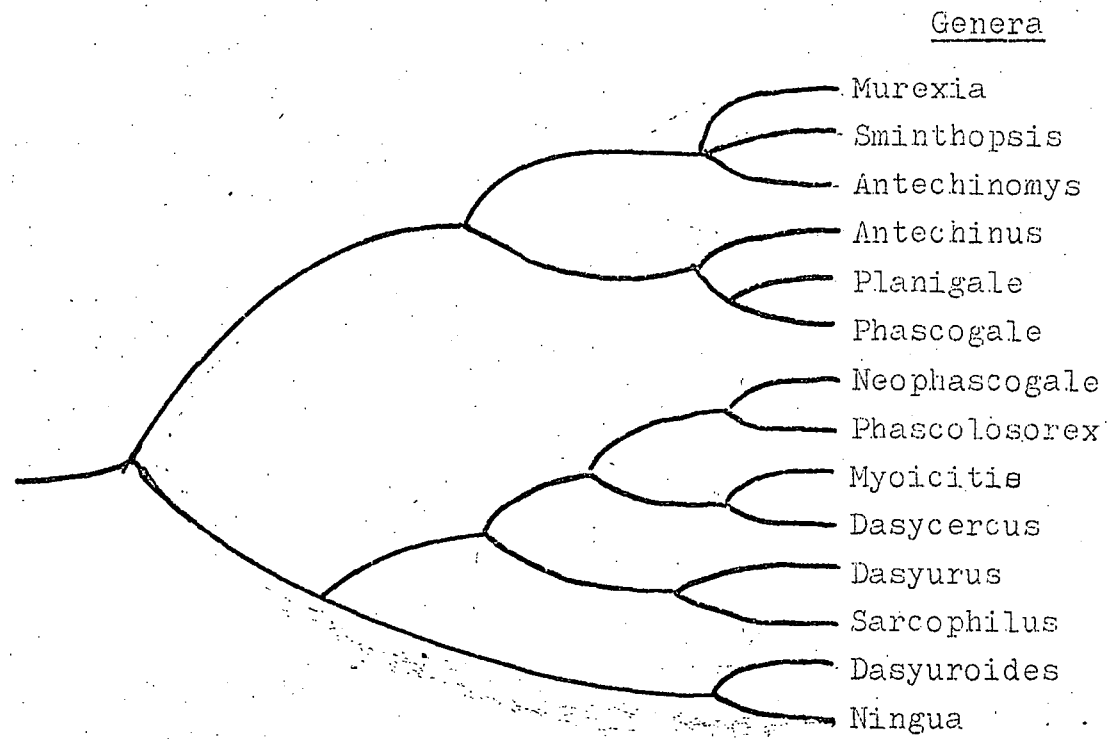


Fig.10 Phylogeny of the Dasyuridae (Modified after Tate (1947)).

Fossils from other Pliocene Pliestocene deposits have been recorded by Longman (1925), Stirton (1957), Marshall (1973).

The Dasyuridae are widely distributed throughout Australia and New Guinea. The genera Murexia, Neophascogale, Phascosorex and Myoicitis are endemic to New Guinea whilst Phascogale, Dasycercus, Sarcophilus, Dasyuraides, Ningui, Sminthopsis and Antechinomys are restricted to Australia. Sarcophilus has recently become restricted to Tasmania.

Summary

The evolution of the Dasyuridae is seen to be a radiation of insectivorous and carnivorous marsupials which have evolved from an Alphadon type of insectivorous ancestor.

The carnivorous adaptation is seen to be correlated with increase in size. Thus the small dasyurids are all insectivorous, terrestrial or arboreal forms whilst the larger dasyurids such as Dasyurus and Sarcophilus are terrestrial carnivores.

The small dasyurids, the Antechinus have been reviewed by Wakefield and Warneke (1963, 1967).

Family Thylacinidae

The Thylacine now restricted to Tasmania, is a large, carnivorous marsupial whose origins are unclear.

Bensley (1903) stated that there are no dental characteristics which could not have been derived from a primitive dasyurid type, although the direction of carnassial development differs from that of the carnivorous dasyurids.

The muzzle in Thylacinus is elongated in contrast to the shortened muzzle of Sarcophilus. The main difference in

carnivorous adaptations in the lower molars, lies in the development of a main posterior shearing crest along the ridge from protoconid to hypoconid, bypassing the metaconid in the Thylacine. In *Sarcophilus*, the shearing ridge which has developed runs from the apex of the protoconid; through the tip of the metaconid to the entoconid, the metaconid is absorbed into this ridge. In both lines the metaconid is reduced, but in the thylacine the shear is developed by accentuating the talonid and hypoconid crest while in the dasyurid line it is developed by specialisation of the metaconid crest with reduction of the talonid (Ride 1964).

It has been concluded, (Tate 1947, Ride 1964, Van Valen 1969) on the basis of its dentition, that the Thylacine evolved from an early dasyurid ancestor.

There is no cytological, serological or reproductive data available on *Thylacinus*.

During the Pliestocene *Thylacinus* was widespread throughout Australia and has been recorded from fossil deposits of New Guinea (Van Deusen 1969).

Ride (1964) from investigation of fossil and modern Thylacine skeletons has concluded that there were possibly four species.

It is thought (Ride 1970) that the Thylacine became extinct on mainland Australia because of competition with the dingo which was introduced there by Aboriginal man some 3000 years ago (Ride 1970).

Family Myrmecobiidae.

This is a monotypic family containing only the banded anteater Myrmecobius fasciatus. There is no fossil record of this marsupial.

The chromosomes of Myrmecobius resemble the dasyurids (Sharman 1961) and it is serologically close to the dasyurids (Kirsch 1968b).

The dentition of Myrmecobius, whilst compatible with that found in other myrmecophagous mammals (Ride 1964) is markedly different from that found in any other marsupials. Generally, Myrmecobius has more molar teeth than other marsupials, Jones (1924) has listed the dental formula as $\frac{4}{3}, \frac{1}{1}, \frac{3}{3}, \frac{5}{6}$, although Bensley (1903) pointed out the great variability of tooth numbers especially of the upper molars.

Bensley concluded that the lower molars could have been derived from the dasyurid type and features of the incisors, canines and premolars indicate affinities with this group. He argued that the dental pattern of Myrmecobius came about by a retrogressive development of already existing teeth with reduplication of teeth from the posterior portion of the dental lamina or the reappearance of formerly vestigial teeth of the same region.

This highly specialised marsupial is adapted to the myrmecophagous habit with long tongue, pointed snout and strong digging limbs with long claws.

ORDER PERAMELINA

The order Peramelina contains some twenty species grouped into two families, the Peramelidae and the Thylacomyidae. While the order is not very diverse, the bandicoots have a wide distribution with eight species being endemic to New Guinea. They are found throughout Australia, including the central arid regions (Keast 1971). In general the Peramelina are terrestrial and adapted to an omnivorous diet, they have strong digging claws and a cursorial, quadrupedal mode of locomotion (Ride 1970).

Origin of the Peramelina

Because of the lack of fossil evidence, the origin of the Peramelina must be deduced from neontological data.

Studies of dentition (Bensley 1903, Tate 1948) reveal that the Peramelina appear to represent an adaption of the insectivorous dentition found in dasyurids and didelphids to a more generalised omnivorous dentition which develops various specialisations in the different genera.

In the unspecialised genera such as Peroryctes, Microperoryctes, Perameles, Rhynchomeles and Echymipera the incisor pattern conforms rather closely with that of the Dasyuridae except that the peramelids retain i^5 which is lost in the dasyurids. As with the Dasyuridae i^1 is distinct, though to a lesser degree, from i^{2-4} , it does not however, erupt late in the peramelids. Features of the incisors which are unique to the Peramelina are the canine form of i^5 and its separation from i^4 . Also the crown of the last lower incisor is bifid.

The premolar pattern of *Microperoryctes*, *Peroryctes longicauda* and *Echimipera rufescens* exhibits the primitive triangular, blade like structure found in the dasyurids, and as with the dasyurids p^4 is larger than p^3 or p^1 . This condition is also found in Didelphidae and Caenoslestidae.

Similarly, the molars of unspecialised peramelids such as *Peroryctes* are almost identical to the tribosphenic molar pattern of the didelphids and the unmodified dasyuridae.

Reproduction in the bandicoots is characteristically polytocous and polyestrous with short gestation, allantoic placentation and the birth of comparatively well developed young. The multiple mammae are enclosed in a backwards opening pouch. (Sharman 1974). The birth canal is long and closes within two days after birth. (Tyndale-Biscoe, 1966). The degree of allantoic placentation is the most developed of all marsupials, in contrast to the yolk sac placentation found in Dasyuridae which is considered primitive (Sharman 1970). Litter size in the *Peramelina* is small compared with the unspecialised dasyurids (Sharman 1970).

The morphology of bandicoot sperm appears to be in between that of the dasyurid type and the phalangerid type (Hughes 1965).

Yadav (1973) found that all polyprotodont marsupials including *Peramelina* have a two to four lobed thoracic thymus and no superficial cervical thymus. All the diprotodont marsupials had both thoracic and cervical thymus.

It appears from this that the *Peramelina* are derived from a primitive dasyurid type of ancestor and Kirsch's (1968b) serological data supports this conclusion. It is for this reason that Kirsch (1975) has chosen to place the bandicoots in

his order Polyprotodonta in the sub-order Peramelomorpha.

The fact remains however, that the Peramelina exhibit syndactyly.

Bensley (1903) concluded that the general type of hind foot in Peramelina represents a derivative of the secondary arboreal phase of the type seen in Phalangeridae. He saw it as a terrestrial adaptation of an arboreal habit with "digitigrade developments for plantigrade ones with a tendency towards functional monodactylism."

In the hind feet of Perameles, Peronyctes, Microperonyctes, and Echymipera there are primitive peramelid features which suggest affinities with the Phalangeridae. These features include a short foot without elongation of digits four or five, the position of the notch separating the conjoined second and third digits from the fourth level with that separating the fourth from the fifth and the presence of slightly curved claws on the fourth and fifth digits. In the more advanced peramelids the claws are stouter and straighter.

More recently, Marshall (1972) has supported the theory that the syndactylous condition seen in peramelids is a modification of that seen in phalangerids. He argued that the tarsal and metatarsal arrangement is the same in dasyurids and phalangerids, and the loss of syndactyly in phalangerids would result in a condition identical to the dasyurid condition. Both the macropod and peramelid foot structures could be derived from the phalangerid arrangement. Marshall suggested that in the peramelids most of the body weight is transferred to the foot via the tibia - astragalus - navicular - ectocuneiform - metatarsal four. This results in the alteration of the

relationships between the cuboid, ectocuneiform and metatarsal four from the arrangement of these bones in a proposed phalangerid ancestor. This modification for transfer of body weight is linked to the quadrupedal mode of locomotion. This arrangement is unique to the Peramelina among the Australian marsupials although placental ungulates exhibit similar modifications for weight transfer.

When all the evidence is combined it is seen that the peramelids have many features, dentition, and serological characters which suggest relationship with the dasyurids. Other features such as chorio-allantoic placentation and sperm morphology are unique to the peramelids. Foot structure is strongly allied with the phalangerids.

In view of this, the most likely interpretation is that the peramelina arose from an early dasyurid line which acquired syndactyly and from which a branch arose which lead to the phalangerids and other diprodonts. (See Fig.11).

Dasyuroidea

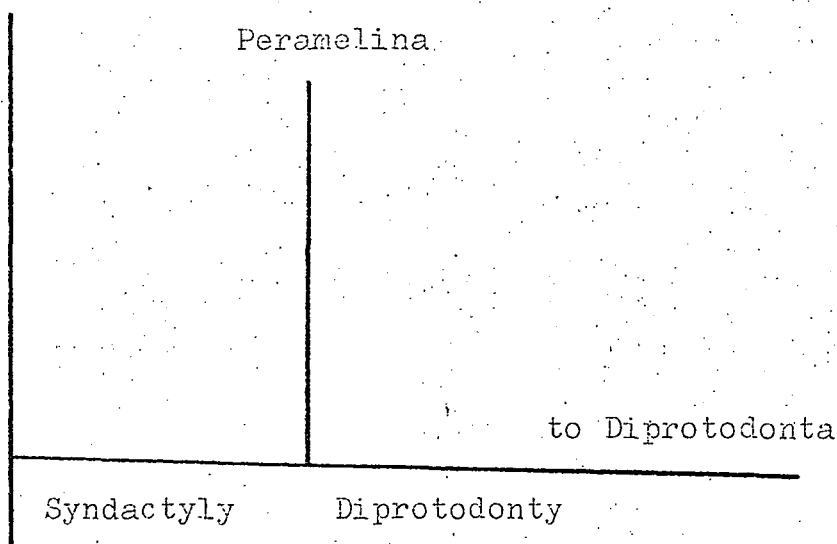


Fig.11 Origin of Peramelina and Diprotodonta from Dasyuroid Ancestors.

This phylogeny is essentially the same as that of Ride (1964).

Evolution within the Peramelina

The evolutionary trend in Peramelina is towards the fossorial, carnivorous, cursorial quadrupedal habit already described.

Dentition (Bensley 1903, Tate 1948)

The most primitive members of the Peramelidae still retain the generalised insectivorous type of dentition seen in the unspecialised dasyurids and didelphids, with even less reduction in incisor formula than is found in the dasyurids.

Omnivorous adaptations are seen in an examination of the premolars (Tate 1948, Bensby 1903). Thus in *Microperoryctes*, *Peroryctes longicauda*, *Echymipera rufescens* the premolar pattern is essentially similar to that of the dasyurids. In *Perumeles*, *Echymipera doreyana* and *Peroryctes raffrayences* p^4 shows the beginning of broadening with the development of an interoposterior ledge. In *Echymipera clara* and *Rhynchomeles* p^4 is greatly enlarged in proportion to the other premolars.

The unmodified genera of Peramelina have the trituberculate molar pattern of the didelphids and unspecialised dasyurids. There is a strong tendency however towards enlargement of the hypocone region of the molars, leading towards a quadrate form in the molars. This trend is noticeable in *Echymipera*, well developed in *Isodon* and most advanced in *Macrotis*. Tate (1948) regarded the development of the quadrituberculate molar as a specialised condition as is the enlargement of the tympanic bulla.

Audital bullae (Tympanic bullae)

Tate (1948) demonstrated that the development of the auditory bullae is an important taxonomic characteristic, (see also Ride 1964 and 1965).

In the *Rhynchomeles*, *Echymipera*, and *Peroryctes* the auditory bullae are quite small with only partial covering of the tympanic ring. In *Perameles* and *Cheoropus* the bullae are larger and almost completely cover the tympanic ring. The enlargement of the bullae is greatest in *Isodon* and *Macrotis*.

Development of the Muzzle (Tate 1948)

Related to the fossorial habit of bandicoots is the elongation of the muzzle. Minimal development is seen in *Isodon* and *Chaeropus* with optimum development in *Rhynchomeles*, *Echymipera clara* and *Macrotis*.

In those species with extreme elongation there are marked differences between the posterior and anterior widths of the palate. In *Rhynchomeles* and *Macrotis* the anterior part of the palate may be only half as wide as the posterior part.

The Ear (Tate 1948, Wood Jones 1925)

In *Perameles*, *Peroryctes* and *Echymipera* the ear is small but not reduced. In *Isodon* the ear is somewhat enlarged and is greatly enlarged in *Cheoropus*. The maximum enlargement is seen in *Macrotis*.

Forelimb (Tate 1948)

In all genera except *Chaeropus* the forelimb with five digits has the third digit longest, the second digit slightly shorter and the fourth digit a little shorter than the second. The first and fifth digits are very greatly reduced.

In *Chearopus*, the "pig footed" bandicoot, the second and third digits are equal in length and function jointly, a condition analogous to the atriodyctyl foot. The fourth is reduced and the first and fifth digits have been lost. It is the structure of the forefoot which sets *Chaeropus* apart from the other peramelids.

Hind Foot (Bensley 1903, Tate 1948)

As previously stated, the development of the hind foot in *Peramelina* represents an adaptation to terrestrial, cursorial, quadrupedal locomotion from an arboreal type found in the phalangerids.

In the bandicoots the fourth digit is always dominant. Somewhat shorter than this is the fifth digit with the syndactylous second and third digits shorter than digit five.

The trend is towards reduction of the first digit. When present, as in *Peroryctes*, *Peramelis*, *Echymipera* and *Isodon*, it is placed well posterior to digits two and three and is short, thick and nailless. In *Chaeropus* and *Macrotis* it is absent and *Chaeropus* has also lost digit five.

Marshall (1972) has described the series *Perameles* - *Macrotis* - *Chaeropus* as steps in the development of the type of weight transfer found in the ungulates. In this condition a great

part of the body weight is transferred to the distal tarsals, bypassing the calcaneum.

The modifications of the hind foot are not totally committed to the cursorial habit but are seen by Marshall to represent a compromise with emphasis on running ability but with provision for the use of hind limbs in digging.

Distribution

When the distribution of the Peramelina is studied it appears that both Australia and New Guinea have sustained independant radiations with some interchange. (See Table 5). Thus *Isoodon* an Australian genera is represented in New Guinea by *Isoodon macroura* and the New Guinea genus *Echymipera* has *Echymipera rufescens* which has entered the Cape York Peninsular from Southern New Guinea. (Tate 1948, 1952; Ziegler 1975).

Paleontology

The only possibly Tertiary fossil bandicoot so far described is *Ischonodon australis* from the Lake Palankarinna formation in South Australia. (Stirton 1955). Stirton described it as being nearer to *Macrotis* than to the Peramelidae, Ride, (1964) is noncommittal with regard to its affinities and states that the only significant feature is its low crowned molars which are lower than are normally found in *Macrotis*.

An undescribed Oligocene bandicoot has been found in the Ngapakaldi fauna of South Australia. (Stirton, Tedford and Woodburne, 1968).

Other fossil material is mostly Pliocene to Recent in age and appears to belong to extant groups. (See Stirton et al 1968, Tedford 1955, Marshall, 1973 and Merrilees, 1973).

Species	Ceram	New Guinea Mountains	New Guinea Lowlands	South New Guinea	Northeast Australia	Northwest Australia	East Australia	Central Australia	Southeast Australia	South Australia	Tasmania	Southwest Australia
Peroryctes												
longicauda		x										
raffrayanus			x									
Microperoryctes												
murina		x										
Perameles												
bougainville								x		x		x
eremiana								x				x
gunnii									x		x	
nasuta					x		x		x			
Echymipera												
elara			x									
kalubu		x	x	x								
rufescens			x	x	x							
Rhynchomeles												
prattorum	x											
Isoodon												
auratus						x		x	x			
macroorus				x	x	x		x	x	x	x	x
obesulus					x		x		x	x		
Chaeropus												
ecaudatus								x				
Macrotis												
lagotis								x	x	x		x
lecura								x				

Table 5. Summary of Distribution of Peramelids
(Tate 1948, Ride 1970, Ziegler 1975).

However, Woodburne (1967) has described a very large bandicoot from the Alcoota Formation in Central Australia. While the damage and wear to the teeth does not allow a definite identification, Woodburne believes the fossil to be moderately close to, though much larger than, *Macrotis*.

Chromosomes

The bandicoots fall into two groups on the basis of chromosome number; in Perameidae $2n=14$, in Thylacomyidae $2n=18q\ 19\sigma$. In the Peramelidae the sex chromosomes are greatly different in morphology and behaviour from any of the other marsupials with $2n=14$. (Hayman and Martin 1969).

The X and Y chromosomes are much larger than those of didelphids, dasyurids and burramyids, and one X chromosome in female peramelids and the Y chromosome of male peramelids is eliminated from most somatic tissues. (Hayman and Martin 1965). In the New Guinea bandicoots *Echymipera kalabu* and *rufescens*, supernumerary chromosomes are found and are seen to be eliminated in the same tissues that eliminate one of the sex chromosomes. (Hayman et al 1969). This elimination of sex and supernumerary chromosomes is known as mosaicism and so far has not been satisfactorily explained.

Hayman and Martin (1969) have suggested that the centromeres of supernumerary chromosomes could serve as donors to acentric fragments formed by breakage of existing chromosomes. Sharman (1973) points out that there is no proof that this method of increasing chromosome number has occurred in the marsupials.

There is no evidence of mosaicism in the Thylacomyidae. The chromosome number $2n=XX/XY, Y_2 + 16A$ is derived by X chromosome autosome fusion and loss of an acentric fragment. Thus, *Macrotis*

is set apart from the Peramelidae on the basis of chromosome number and chromosomal sex determination. Factors such as this would seem to justify Kirsch's (1975) raising of the Thylacomyidae to family level.

Summary

The Order Peramelina has two main lines of evolution, the Peramelidae and the Thylacomyidae. Evidence for this comes from comparisons of chromosomes and examinations of molar and tympanic bullae development.

Within the Peramelidae, Chearopus is set apart by the extreme modification of the feet and ears. In the unspecialised New Guinea group, Percryctes, Micropercryctes, Echymipera and Rhynchomeles, Echymipera and Rhynchomeles have both lost i^5 and in Rhynchomeles the elongation of the rostrum is extreme.

Perameles differs from the New Guinea group in the degree of enlargement of the tympanic bullae.

Isoodon exhibits great enlargement of the tympanic bullae with fairly advanced development of the quadrate molar. Elongation of the rostrum is minimal in Isoodon.

Fig. 12 is a summary of the phylogeny of the Peramelina adapted from Tate (1948).

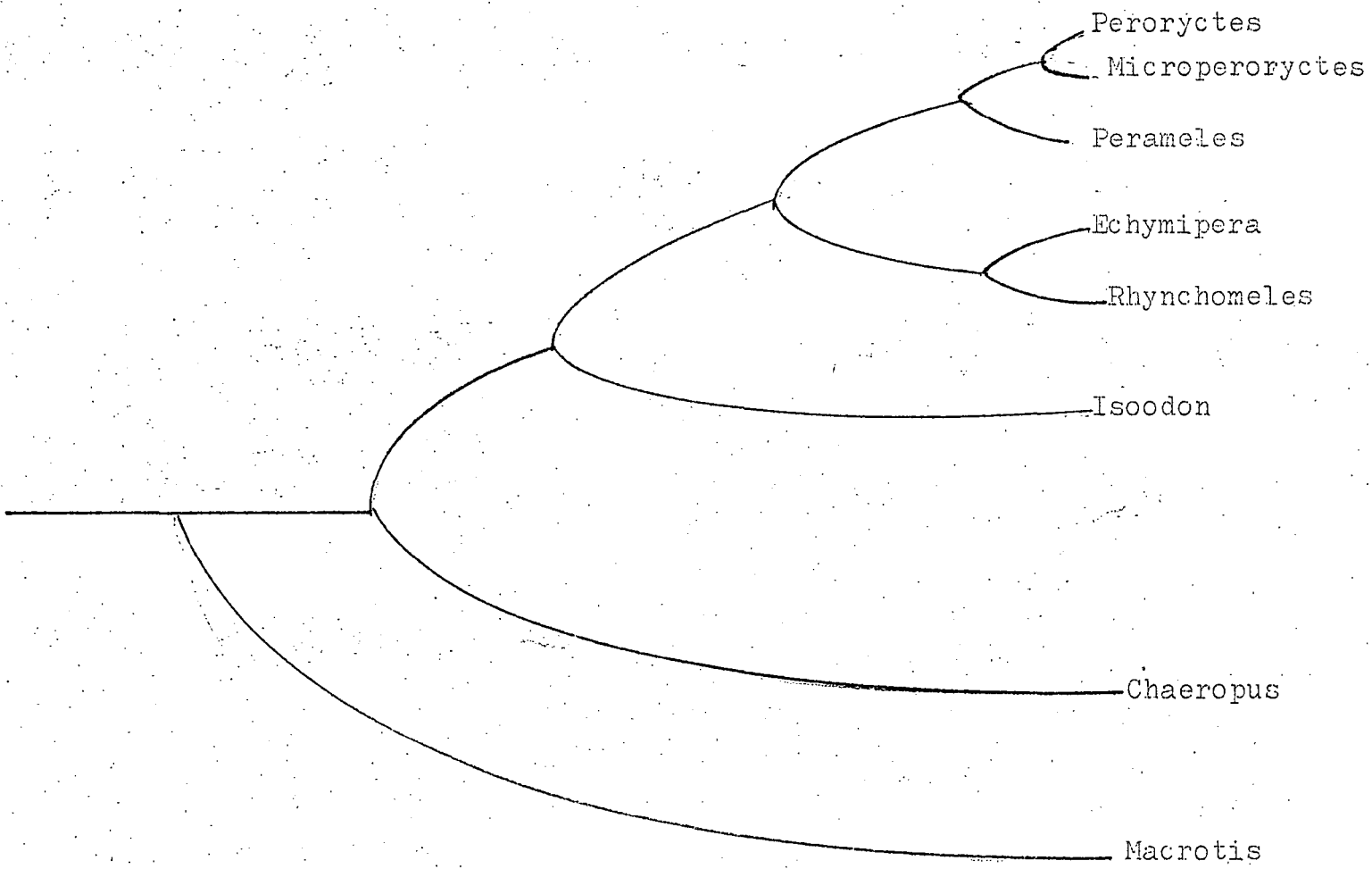


Fig. 12 Phylogeny of the Peramelina (modified after Tate 1948, 1952, Ziegler 1972 and Kirsch 1975).

EVOLUTION OF THE DIPROTODONTA

Origin of Diprotodonty

Diprotodonty is found in the Australian Order Diprotodonta and in the South American Order Paucituberculata. This led to the suggestion (Osgood 1921) that the caenolestidae were related to the Australian Phalangeroidea. Since then it has become clear that caenolestids are in no way related to any Australian forms. (Obenchain 1925, Biggers et al, 1965, Hayman et al, 1971). The results of Hayman et al suggest that the Caenolestidae are no more closely related to any Australian marsupials than they are to the Didelphidae. It must be concluded therefore that diprotodonty has arisen twice in marsupial evolution.

Bensley (1903) argued that the diprotodont modification, although characteristic of the herbivorous marsupials, "is the result of an insectivorous adaptation which developed in the incipient stages of the omnivorous evolution, but after the separation of the peramelid stem."

The development of the diprotodonty involved the following modifications:-

1. Reduction in upper incisor from five to three or even one.
2. Reduction of lower incisor formula to one.
3. Enlargement of median incisors.
4. Reduction and ultimate loss of lateral incisors, canines and anterior premolars.

As mentioned previously (p.43) emphasis is placed on the development of i^1 in the dasyurids, especially in the unmodified insectivorous genera such as *Phascogale* and *Antechinus*. This grasping, piercing modification of i^1 increases the animal's ability to capture and hold its insect prey. In the *Dasyuridae* there is no corresponding modification of the lower median incisors. In certain phalangeroids, such as *Distoechurus*, this modification of the upper incisors is seen together with a modification of the lower teeth to allow the upper and lower median incisors to meet somewhat in the manner of the points of a pair of forceps.

Bensley argues that development of the lower median incisors in an unmodified insectivorous dasyurid, to correspond with the development of the median upper incisors would result ultimately in the diprotodont condition observed in the *Phalangeroidea*.

Firstly, elongation of the lower median incisors would result in shortening of the anterior portion of the lower jaw in order that the upper and lower median incisors would meet. This would displace the areas of contact between the upper and lower anterior teeth. There would be a tendency for reduction or loss of the lower incisors immediately posterior to the enlarged median incisors.

Secondly, there would be a reduction in the number of posterior upper incisors, since only those teeth which came into contact with the median lower incisors would persist.

In *Distoechurus*, while the lower molars and the posterior and median premolars are in the normal condition with regard to the upper teeth, at least two teeth, possibly the first premolar and the canine have been lost. In all phalangeroids the number

of upper incisors is reduced to three, with the lateral two together serving as a stop for the enlarged lower teeth.

The diprotodont condition is seen then as an insectivorous modification from which arose the herbivorous condition seen to-day in many marsupials within the Diprotodonta.

Origin of the Diprotodonta

The origin of the Diprotodonta has already been discussed in the previous section and in the discussion of the origin of the Peramelina (p.51).

The ancestors of the Diprotodonta were seen to be derived from the insectivorous, syndactylous line which led to the Peramelina. The branch in which diprotodonty arose led to the arboreal phalangerids and these are thought to represent the ancestors of the herbivorous diprotodonts.

Evolution within the Diprotodonta

The Diprotodonta contains marsupials exhibiting a wide variety of habits and morphological forms. There are thought to be at least five distinct phyletic lines.

The Phalangerioidea which contains the Burramyidae; Petauridae and the Phalangeridae which are collectively known as the possums and gliders. The Macropodidae which contains the kangaroos and wallabies is a separate morphological line and is also contained within the Phalangerioidea. The superfamily Vombatoidea contains the Vombatidae, wombats, and the Phascolarctidae, koalas. There are also two extinct families, Wynyardidae and Diprotodontidae. The aberrant Tarsipes spenceri has been placed in a separate monotypic family Tarsipidae (Ride 1964, 1970, Kirsch 1975).

SUPERFAMILY PHALANGEROIDEA

This superfamily contains the majority of the Australian marsupials and is the main stem of the diprotodont radiation.

Primitively, the Phalangeroidea arose from small, insectivorous, arboreal syndactylous diprotodonts (Bensley 1903) (which probably shared some characters with Wynyardia (Ride 1964)).

Bensley saw the diprotodont radiation as a sequence where firstly the insectivorous characteristics were modified in favour of an omnivorous habit and once this omnivorous modification was complete, then specialisations were developed from it in several different lines. He traced the dental evolution of the various lines in detail and supported his conclusions by examination of comparative foot structure.

The dental evolution of the Phalangeroidea firstly involved the development of the omnivorous dentition of the type seen in the Petauridae and Phalangeridae. There have been some aberrant insectivorous developments such as *Burramys* and *Dactylopsila*. *Thylacoleo* represents a carnivorous modification of the omnivorous dentition.

Once the modifications necessary for an omnivorous diet were complete, the phalangeroid stock gave rise to the specialised herbivores. *Trichosorus* and *Phalanger* are arboreal herbivores, these genera have evolved the selonodont dentition to facilitate the chewing of leaves and shoots. From the arboreal omnivores were derived the terrestrial herbivores, the macropods.

The primitive phalangeroids derived their dental pattern from the primitive insectivorous dasyurid type. In the *Burramyidae* which is considered the least specialised family of the Phalangeroidea, the evolution of bunodont molars is fairly advanced. The diprotodont incisor sequence is of insectivorous type with

procumbent, piercing median incisors and reduced upper lateral incisors. (There are no lower lateral incisors in diprotodont marsupials). The canines are still present and functional as in the dasyurids. The premolars are of a piercing insectivorous form with reduction of the posterior upper teeth. The lower premolars are reduced in number, with only the median and posterior teeth functional.

In Petauridae which has evolved towards omnivory, the bunoid condition of the molars is advanced with some indications of transverse ridging on the upper molars. The incisors are similar to those of Burramyidae. The canines in Petauridae are shorter than in Burramyidae and somewhat compressed. The premolars generally are reduced. In Petaurus the upper anterior and median premolars are low and the median teeth are reduced. The upper posterior premolars are moderately developed with a tendency towards grooving on the outer edge. The lower posterior premolars are reduced and may be slightly grooved on the edge. In Dactylopsila the premolars are generally more reduced than in Petaurus with the exception of the upper anterior premolars which show subcaniniform development.

In Phalangeridae, the bunoid upper molars are oblong in shape with all cusps of the same height and with sharp ridging on the outer cusps. This is seen to be an arboreal herbivorous adaptation of the condition seen in Petauridae. In the lower molars the lophodont development corresponds with the upper molars. Of the incisors of Phalangeridae there are no insectivorous indications. These herbivorous modifications which are also seen in the Macropodinae, involve the reduction of the upper median incisors so that they become more rounded in section and only slightly longer than the lateral incisors. The lateral incisors resemble those of Petauridae, although some

species of Phalanger have the third upper incisors reduced and displaced by encroachment of the canines. The lower incisors are flattened, lanceolate and only slightly curved. The canines are reduced in *Trichosurus* and in some members of Phalanger. In other species of Phalanger however, they are secondarily enlarged. The premolars are further reduced in the Phalangeridae with the exception of the upper and lower posterior premolars which tend towards sectorial development. As in the Phalangeridae, the molars of the macropodid sub-family Potoroinae are quadrituberculate and slightly lophoid. The upper median incisors are enlarged and elongated and resemble some species of the *Petauridae*. The tips of the lateral incisors are turned inwards to act as a stop for the lanceolate lower incisors. Canines are reduced but not completely vestigial in the Potoroinae.

In the Macropodinae the molars are definitely lophodont with transverse crests connecting the anterior and posterior cusps. The median upper incisors are shortened and rounded with slightly flattened tips. They project slightly beyond the lateral incisors which are small and appear to be grasping as well as cutting organs. The lower incisors are lanceolate with cutting edges. In the Macropodinae, the canines are present in a reduced condition in *Dendrolagus* and *Dorcopsis* and are absent in all other genera.

The premolars, both in morphology and number are variable throughout the Macropodidae (see also Bartholomai 1971).

In the Macropodidae there is a large diastema between the upper incisors and first functional premolars in the Macropodinae in comparison with the Potoroinae. The molars of the Potoroinae are reduced in size posteriorly and have a fixed position in the jaw, whereas in the Macropodinae they are equal in size and more forward in the jaw. They are shed progressively

from the front and are replaced by posterior late erupting molars.

In the Phalangeroidea, the lower teeth, between the median incisors and the median premolars are generally vestigial. In Burramyidae the median premolars are retained as a piercing organ. In Petauridae and to a greater extent in Phalangeridae and Macropodidae these⁵ premolars have become modified as sectorials.

In some respects the incisors of the macropodinae resemble those of the browsing Equidae. Also, with the exception of *Hypsiprymnodon*, the macropods have converged upon the eutherian ruminants in having evolved an efficient form of ruminant digestion (Tyndale-Biscoe 1972)

Summary (see Fig. 13)

The phalangeroid radiation is seen to have evolved from an arboreal ancestral form which, while diprotodont, exhibited a similar type of insectivorous dentition to that found in the insectivorous dasyurids. The Burramyidae family is a present day derivative of this form. The evolution of an omnivorous dentition permitted the exploitation of a wider range of available food and the family Petauridae is seen to be representative of the generalised omnivorous adaptation.

Once the omnivorous pattern was established, various adaptations to different habitats took place. The evolution of arboreal and terrestrial herbivores involved reduction and modification of the omnivore dental pattern as did the evolution of certain insectivorous types.

The ancestor of the extinct, carnivorous diprotodont *Thylacoleo* is thought to have been a herbivorous phalangeroid and this will be discussed in a later section.

This phylogenic derivation of the Phalangeroidea is supported by evidence from comparative foot morphology (Bensley 1903, Marshall 1972) and serology (Kirsch 1968b).

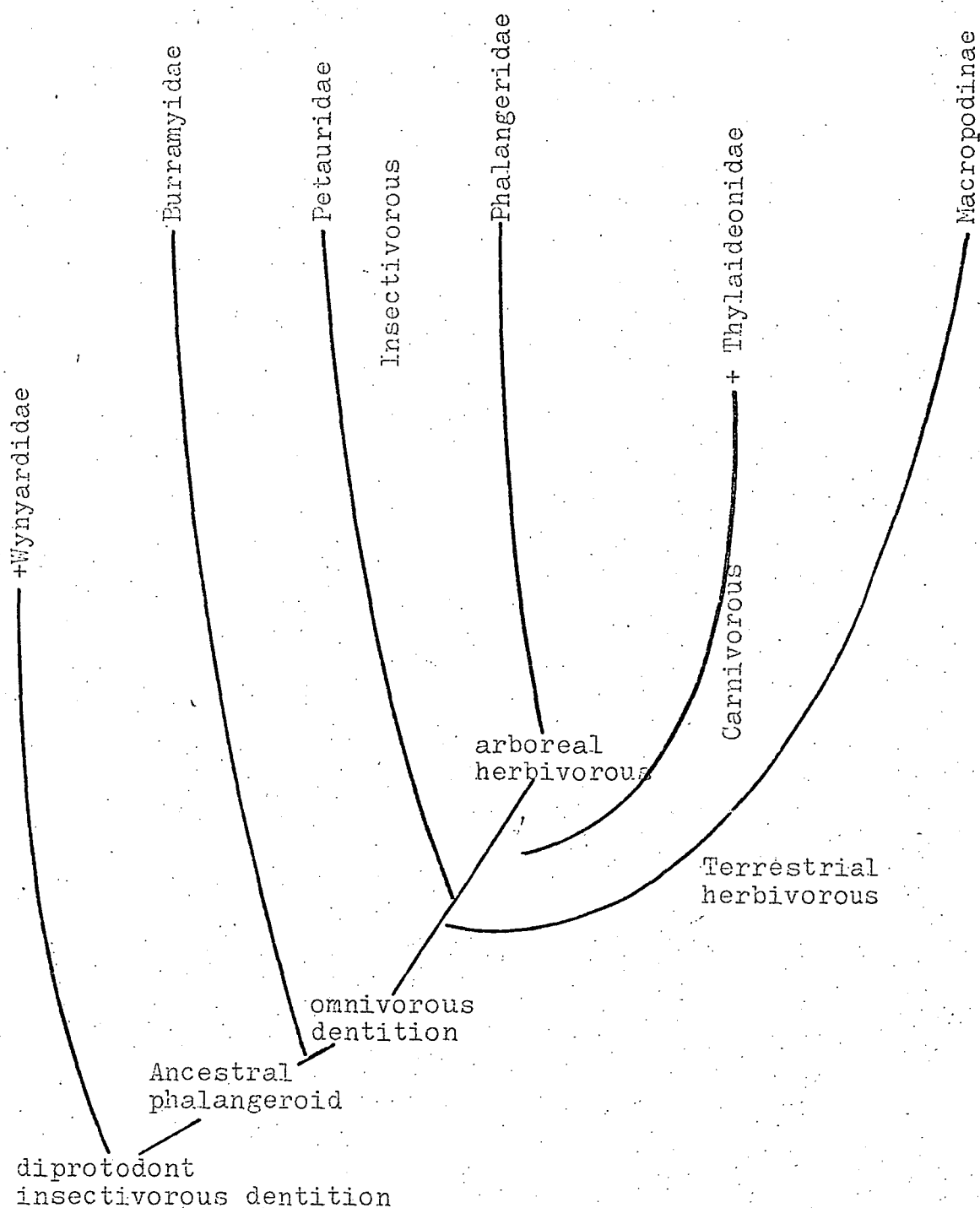


Fig. 13. Phylogeny of the Phalangeroidea.

(Bensley 1903, Tate 1945a,b,c, 1948, Woods 1961, Ride, 1964).

Family Wynyardidae

The family Wynyardidae was erected (Osgood 1921, Ride 1964) to accommodate the late Oligocene - early Miocene (Gill 1962, Quilty 1966) fossil *Wynyardia bassiana*. (Spencer 1901, Wood Jones 1931).

Ride (1964) has re-examined this fossil, which is remarkably complete, and has noted that as well as being a diprotodont, it exhibits many primitive didelphoid features. Other features are interpreted as being specialised adaptations.

The diprotodont features include the presence of the paired single incisors at the anterior ends of the mandibles and the typically diprotodont position of the zygomatic arch.

The structure of the middle ear region, though incomplete in the fossil, indicates that the tympanic ring was not tubular and fused to the post-glenoid process as in the Diprotodonta. Ride suggests that the condition of the postero-mesial end of the post-glenoid process indicates that this was the point of contact of the tympanic ring. This would indicate an intermediate stage between the free ring of the Didelphidae and the fused tube found in the Phalangerioidea.

The complete absence of the epitympanic sinuses either anterior or posterior to the epitympanic recess in *Wynyardia* is a primitive condition found in didelphids and monotremes. The epitympanic recess is very small and the broken portion of the allisphenoid which remains suggests that the allisphenoid bulla was very short and merely shielded the epitympanic recess. The appearance of the entire region resembles that of *Didelphis virginiana*.

Other marsupicarnivoran characteristics are the didelphoid shape of the nasals, the lachrymo-nasal contact, the great saggital crest, the very short post tympanic region and the position of the sacral articulation in the ilium. The triangular cross section of the ilium is also typically Didelphis-like.

Other features which are specialised in Wynyardia are related to its robust build and probably erect carriage. They appear to be largely of a form compatable with the Phalangeroidea.

Wynyardia is seen as an early offshoot of the mainstem of the Diprotodonta which is represented by the Phalangeroidea. The primitive features of Wynyardia would probably have been present in the ancestral diprotodont stock.

Family Burramyidae

The family Burramyidae is presently composed of seven species representing four genera, three of which are monotypic (Kirsch 1975).

Cytological studies reveal the burramyids to be a discrete group of diprotodonts. In so far as they have been studied they all have a chromosome number of $2n=14$ with a sex chromosome pattern of XX/XY. There are small morphological differences between chromosomes of Burramys and Acrobates with greater differences between these two and Cercartetus. The family, however, is quite distinct from all other phalangeroids.

There are similarities between the sex chromosomes of the burramyids and the dasyurids and some American marsupials (Gunson et al, 1968).

Serological studies (Kirsch 1968(a)) show that Burramys, Cercartetus and Acrobates are closer to each other than to any other phalangeroids.

Cytological and serological studies have not been carried out on the New Guinea genus *Distoechurus*.

With the exception of *Cercartetus concinnus*, little is known about the reproductive physiology of the Burramyidae.

C. concinnus is polyestrous and polytocous. At birth, the young are comparable in size to new born *Antichinus* and are born by way of a temporary pseudo-vaginal canal (Clark 1966). Clark has also noted a high degree of reproductive wastage compared with other phalangeroids, this is a primitive feature found in dasyurids.

Bensley (1903) considered the members of this family to be the most primitive of all diprotodonts. He included the burramyids in the sub-family Phalangerinae along with most of the members of the present day Phalangeridae and Petauridae. He did not include *Burramys* in his discussion as it was known only as a fossil at that time and was thought to represent a link between phalangers and kangaroos (Broom 1896(a)) or to be ancestral to the *Thylacoleo* (Broom 1898).

Bensley also discussed a genus known as *Dromicia*. Species of this genus are now included in the genus *Cercartetus* (Iredale and Traughton 1934, Wakefield 1963, Ride 1964(b)).

The trend in Burramyidae is towards reduction or loss of m_{11}^4 . It is least reduced in *Cercartetus lepidus*, and greatly reduced in *C. caudatus* and *Burramys*. It has been lost in *Acrobates*, *Distoechurus*, *C. concinnus* and *C. nanus* (Bensley 1903, Ride 1956, Wakefield 1966).

Bensley considered *Distoechurus* to be the least modified burramyid. In *Distoechurus* the upper molars decrease in size from anterior to posterior, the first tooth being three times as large as the third. The shape of the upper molars is triangular

due to underdevelopment of the hypocone and, in respect of the position of the hypocone and protocone, resemble the peramelids and dasyurids. The difference between the dasyurids and peramelids and the burramyids is seen in the bunoid development of the metacone and paracone. There are no external styles, nor is there a metacone spur.

The lower molars do not show such a marked gradation in size as the upper molars. The first lower molar is only slightly larger than the second which is slightly larger than the third.

The second and third lower molars are oblong and quadrituberculate with only the protoconid, metaconid, hypoconid and entoconid present. The protoconid and hypoconid are not completely bunoid and retain a primitively triangular section. These two cusps are separated externally by an angular notch. The anterior and posterior margins of each tooth bear a small ledge connected with a fine ridge running over the tips of the outer cusps. This ledge, minute in *Distoechurus* becomes more prominent in the more advanced phalangeroids.

The first lower molar in *Distoechurus* is modified to a somewhat canine form, with the metaconid reduced to form a small tubercle on the inner side.

The molars of *Acrobates* resemble those of *Distoechurus* but the upper teeth are more quadrate and the size gradation is less marked. In the first lower molar the canine form found in *Distoechurus* is not so well developed and the metacone is not so reduced.

In *Cercartetus*, the anterior upper molars are quadrate like those of *Acrobates*, except for *C. concinnus* which resembles

Distoechurus. The third upper molar is triangular and trituberculate as the hypocone is absent.

The first lower molar of C. concinnus resembles that of Distoechurus with loss of the metaconid. The metaconid is absent in C. nana. In C. lepidus the first lower molar resembles that of Acrobates.

Burramys has similar molar tooth structure to Distoechurus with the exception of a pair of large grooved sectorials, reduced fourth molars and elongate incisors. Ride (1956) considers the dental modifications seen in Burramys to be a peculiar insectivorous or microcarnivorous adaptation.

Burramys is larger than any of the other burramyids (Ride 1970) and as Bensley and Van Valen (1969) have pointed out, increase in size in a predatory group is accompanied by increased development of carnivorous modifications.

Of the Burramyidae, only Acrobates has developed a gliding membrane. (Tate, 1945(c)). The entire family possesses a prehensile tail with variations in shape, fur cover and length exhibited in the various species (Tate 1945(c)).

The two most southern ranging species, Cercartetus nanus and C. lepidus have both evolved the seasonal deposition of subcutaneous fat.

The genus Cercartetus was proposed by Wakefield (1966) to include all of the pygmy possums which were previously placed in two genera, Cercartetus and Eudromicia (Iredale and Traughton 1934). Wakefield assigned them to a single genus on the basis of:-

1. The development of the tympanic bullae. It is equally swollen in C. nanus and C. concinnus, less

swollen in C. lepidus and only slightly swollen in C. caudatus.

2. The squamosal inflation which is greatest in C. concinnus, less in C. nanus, less in C. caudatus and least in C. lepidus.
3. The similarity in development of p^4 in all species.
4. The variability of morphology of the small upper premolars seen in individuals of any one species.
5. The variability of the molar pattern.

Wakefield's decision to include all of the pygmy possums in a single genus rather than classifying them as four separate monotypic genera has been challenged by Turnbull and Schram (1973). On the basis of studies of dental morphology of two species C. nanus and C. caudatus from the breccia of the Broom cave they concluded that these two species were sufficiently different to warrant being placed in different genera.

Distribution studies show that the majority of Burramyidae are found on the Australian continent. Two species of Cercartetus, C. nanus and C. concinnus, extend south into Tasmania. Two genera, represented by two species, Distoechurus pennatus and Cercartus caudatus are found in New Guinea, and Distoechurus is endemic (see Table 6).

It appears from this that the Burramyidae are primarily a continental Australian radiation with dispersal of the southern forms into Tasmania, and an entry into and subsequent minor radiation in New Guinea.

Genera and Species										
	New Guinea Mountains	New Guinea Lowlands	South New Guinea	Northeast Australia	Northwest Australia	East Australia	Central Australia	Southeast Australia	South Australia	Tasmania
Cercartetus caudatus	x			x						
concinus									x	
lepidus								x		x
natus								x		x
Distoechurus pennatus		x								
Acrobates pygmaeus				x		x		x		
Burramys parvus								x		

Table 6 . Distribution of Burramyidae. (Tate 1945, Wakefield 1966, Ride 1970).

Summary

The family Burramyidae is seen as an insectivorous diprotodont derivative of the unspecialised dasyurid form. The members of this family are closely related to each other serologically and cytologically.

Distoechurus is the most representative of the unmodified ancestral form, with Cercartetus showing dental characters intermediate between it and Acrobates.

Acrobates, whilst dentally similar to Distoechurus has evolved a gliding membrane which sets it apart from the other members of the family.

Burramys, the largest of the Burramyidae is seen to be a derivative of the basic Distoechurus type with specialisations which emphasise an insectivorous or microcarnivorous diet.

The genus Cercartetus is a much broader genus than the other genera. It has been suggested the four species belonging to this genus are dissimilar to the extent that they should themselves be raised to the level of genera.

The southern forms of Cercartetus which are found in Tasmania and southern Australia have evolved seasonal subcutaneous fat deposition, presumably in response to colder winters.

Studies of distribution suggest that Burramyidae are a mainland Australian radiation with southern dispersal into Tasmania and northern dispersal and a minor radiation in New Guinea.

Family Petauridae

The family Petauridae contains the ring tail possums and the gliders. There are twenty-two species recognised at present and there is some confusion regarding genera and sub-genera (Kirsch 1975).

Unlike the Burramyidae, the Petauridae have variable chromosome numbers. Petaurus breviceps and Schinobates volans have chromosome number $2n=22$. Pseudocheirus peregrinus has $2n=20$ while Pseudocheirus archeri has $2n=16$. Pseudocheirus (Hemibelideus) lemuroides has $2n=20$. Of all species studied, the sex chromosome complement is XX/XY (Hayman and Martin 1969).

From studies of the morphology of the chromosomes, Hayman and Martin consider that the karyotype of Pseudocheirus (Hemibelideus) lemeuroides is probably derived from a chromosome complement similar to that seen in Schinobates. They suggest that Pseudocheirus archeri also arose by chromosome reduction from $2n=22$. It appears that the basic chromosome number for this family is $2n=22$. This would set the family apart from Burramyidae and also Phalangeridae, where it is possible that the primitive chromosome number is $2n=14$ (Hayman and Martin 1969).

Serological studies (Kirsch 1968a) show that Schinobates, Pseudocheirus and Petaurus are associated more closely with each other than with any other phalangeroids.

Investigations of reproduction in Schinobates (Smith 1968) and Pseudocheirus peregrinus (Sharmon 1959, Hughes 1965) have shown that breeding is seasonal with regression of the testes following the end of the breeding season. In Trichosurus (Phalangeridae) sperm production is continuous.

The female reproductive tracts of *Schinobates* and *P. peregrinus* are similar, although more primitive features are found in *Schinobates* (Smith 1969). *Schinobates* is polyestrous and monovular which is an advanced condition compared with *Burramyidae*.

Bensley (1903) believed, on the basis of molar pattern, that *Gymnobelideus* represented the most primitive condition in this family. The molar pattern is unreduced with decrease in size posteriorly. The upper molar pattern is similar to *Cercartetus*. *Petaurus* the genus in which gliding membranes have been evolved, resembles *Gymnobelideus*.

Bensley argued that in the Family *Burramyidae* a trend towards an omnivorous dentition from the insectivorous condition was observed. In *Petauridae*, this trend is seen but at a more advanced stage than in *Burramyidae*. In *Gymnobelideus*, the insectivorous condition has many omnivorous characters. Bensley believed that in *Petaurus* the dentition was completely adapted to the omnivorous condition.

Dactylopsila which includes animals which are considerably larger (Ride 1970) than those of the preceding genera is thought by Bensley to be close to *Gymnobelideus* in its affinities. However, it is aberrant in its development of dental modifications which are more suited to an insectivorous habit. As well as dental modifications, *Dactylopsila* has an elongated second digit of the manus which is used for extracting insects from under the bark of trees (Ride 1970).

Bensley separated the genera *Pseudocheirus* and *Schinobates* from the preceding genera because of the selonoid development of the cusps of the molars and the presence of external styles on the upper teeth. He included them with

Phascolarctos in the sub-family Phascolarctinae. He believed them to share common ancestry with the Petauridae on the basis of incisors, premolars and foot structure.

Recently however, it has been shown that Phascolarctos is more closely allied with Vombatidae (Traughton 1956, Kirsch 1968).

Pseudocheirus and Schinobates are now included in the family Petauridae because of similarities of sperm morphology (Biggers 1966) serology (Kirsch 1968a) and cytology (Hayman and Martin 1969).

Of Pseudocheirus and Schinobates, Bensley pointed out that they are almost identical in dentition and he concluded that Schinobates was simply a volant form of Pseudocheirus.

Pseudocheirus is a large genus with three subgenera, at present, containing some thirteen species (Kirsch 1975). They are widespread, being found throughout Australia, Tasmania and New Guinea. The greatest radiation occurs in New Guinea and northern Australia, see Table .

Tate (1945b) has shown that in New Guinea, Pseudocheirus inhabits mountainous country and is found in isolated populations composed of three or more different species. There are no species which occur in both New Guinea and Australia, and Tate believes that this is possibly because of the New Guinea species' preference for high altitudes. Tate has also suggested that the Australian radiation has been limited by the lack of mountainous areas.

The Tasmanian Ringtail, previously known as P. convolutor has been shown by Kirsch (1968b) to be the same species as P. peregrinus of mainland Australia.

It appears that two radiations of *Pseudocheirus* have taken place in New Guinea and Australia, since both *Pseudocheirus* (*Pseudocheirus*) and *Pseudocheirus* (*Pseudochirops*) have species endemic to Australia and New Guinea.

Schinobates volans is restricted to Eastern Australia from Queensland to Victoria.

Dactylopsila is mainly a New Guinea genus with one species *D. trivirgata*, represented in northern Australia.

Petauroides is primarily an Australian radiation with only *P. breviceps* occurring in both New Guinea and Australia.

Gymnobelideus is presently restricted to southern and southeastern Victoria.

Summary

The family Petauridae generally represents an omnivorous modification of the insectivorous type diprotodonty seen in the unspecialised Burramyidae. It is likely that these families shared a common insectivorous diprotodont ancestor.

Gymnobelideus and *Petaurus* share many primitive features of the group. *Dactylopsila* is seen as a specialised offshoot of the group which has modifications in keeping with a predaceous insectivorous habit.

Pseudocheirus and *Schinobates* are evolved herbivorous modifications.

It is noted that gliding membranes have evolved in three separate groups of possums. In the family Burramyidae, *Acrobates pygmeus* is most closely related to the non volant genera *Distoechurus* and *Cercartetus*. In Petauridae, *Petaurus* is closely allied with *Gymnobelideus* and *Schinobates* is most closely related to *Pseudocheirus*.

Genera Species	New Guinea Mountains	New Guinea Lowlands	South New Guinea	Northeast Australia	Northwest Australia	Central Australia	Southeast Australia	South Australia	Tasmania	Southwest Australia	East Australia
Gymnobelideus											
leadbeateri							x	x			
Petaurus											
australis				x			x				
breviceps	x	x	x	x			x				x
norfolcensis				x			x				x
Pseudocheirus											
(Pseudocheirus)											
canescens	x										
caroli	x	x	x								
forbesi	x										
herbertensis				x							
mayeri	x										
peregrinus					x		x	x	x		x
schlegeli											
(Pseudochirops)											
albertisii			x								
archeri				x							
corinnae	x										
cupreus	x										
dahli					x	x					
(Hemibelideus)											
lemuroides				x							
Schinobates											
volans				x			x				
Dactylopsila											
(Dactylopsila)											
megalura	x	x	x								
tatei	x	x	x								
trivirgata	x	x	x	x							
(Dactylonax)											
palpator	x	x	x								

Table 7 . Distribution of the Family Petauridae (after Tate 1948b, 1948c; Ride 1970).

Family Phalangeridae

The family Phalangeridae contains the brushtail possums, the scaley tail possum and the cuscuses.

Serologically, the members of Phalangeridae which have been studied, Phalanger, Trichosurus and Wyulda (Kirsch 1968a) are closer to each other than to Petauridae or Burramyidae.

Cytological studies have shown that chromosome number is variable but Hayman and Martin (1969) suspect that the primitive karyotype may resemble that found in Burramyidae with $2n=14$.

There are presently eleven species recognised as belonging to this family and they are grouped into three genera, Trichosurus, Wyulda and Phalanger (Kirsch 1975).

On the basis of dentition, Bensley (1903) considered that Phalangeridae resembled Petauridae but with more herbivorous modifications especially in Trichosurus.

This herbivorous trend is seen in the oblong, quadrate posterior molars with their sharply ridged upper outer cusps and lower inner cusps. The ridging is more conspicuous in Trichosurus.

The median incisors are reduced so that their tips project only slightly beyond the lateral teeth in Phalanger. In Trichosurus the median incisors are the same size as the lateral teeth. In both genera the lower incisors are flattened lanceolate and only slightly curved.

The canines in Phalanger ursinus are about the same size as the third incisors, in Trichosurus they are slightly smaller than the third incisor. In other species of Phalanger, the canines are enlarged and present the characters of normal canines.

The posterior premolars are enlarged as sectorials with one or two grooves in Phalanger. The trenchant edge is elevated and in some phalangers such as P. orientalis the trenchant edge is rotated and the tooth is enlarged.

In Trichosurus the sectorial posterior premolars are similar to those in P. orientalis and show signs of having three grooves. The sectorial teeth of Trichosurus generally show more wear than those of Phalanger which supports the conclusion that Trichosurus is a more advanced herbivore than Phalanger.

Trichosurus and Phalanger differ in gross morphology, Trichosurus exhibits a bushy tail while the tail in Phalanger is semi naked. Wyulda has a tail which is bushy at its base and then hairless for the greater part of its length and covered with a mosaic of scales. The ears of Wyulda are small compared with Trichosurus (Ride 1970).

Wyulda is found only in the region of the Kimberly and inhabits trees in rocky country as well as spending much of its time among sandstone rocks. It is obviously adapted to this type of terrain and occurs nowhere else (see Table).

Trichosurus is widespread throughout mainland Australia and Tasmania (Ride 1970).

Phalanger is primarily a New Guinea genus, however there are two species, P. maculatus and P. orientalis which are found on the Cape York peninsular. These species also occur in New Guinea. Thus Trichosurus and Wyulda represent the Australian radiation of Phalangeridae and Phalanger represents the New Guinean radiation. Tate (1945a) has examined the Phalanger radiation and the geographical distribution of this genus.

Genera Species	New Guinea Mountains	New Guinea Lowlands	South New Guinea	Northeast Australia	Northwest Australia	Central Australia	Southeast Australia	South Australia	Tasmania	Southwest Australia	East Australia	Celebes
Trichosurus												
arnhemensis						x						
caninus												
vulpecula				x	x		x	x	x	x	x	
Wyulda												
squamicaudata						x						
Phalanger												
atrimaculatus	x											
celebensis												x
gymnotis	x											
maculatus		x	x	x								
orientalis		x	x	x								
ursinus												x
vestitus	x											

Table 8 . Distribution of Phalangeridae (after Tate 1945(a), 1952; Ride 1970).

Investigations of reproduction in this family have been restricted to Trichosurus vulpecula (Kean 1961, Kean et al 1964, Pilton and Sharman 1962). It is polyestrous and monotocous, or polytocous, with a gestation period which is considerably shorter than one estrous cycle. The pseudovaginal canal is very short compared with Schinobates (Smith 1968) and is formed anew for each parturition (Pilton and Sharman 1962).

Summary

The Phalangeridae are large herbivorous possums which are thought to be derived from a more omnivorous type. They have no dental similarities with members of Petauridae and most

closely resemble Burramyidae in karyotype.

Of the Phalangeridae, *Trichosurus* and *Wyulda* represent the Australian radiation with *Wyulda* being an isolated monotype genus. The genus *Phalanger* is a New Guinean radiation of which two species have invaded northern Queensland.

Family Thylacoleonidae

This family contains the two known species of extinct marsupial lion Thylacoleo. T. crassicaudata is known from Pliocene Chinchilla Sand deposits (Bartholemai 1962) and T. carnifex is the typical Pliestocene form which appears to be more highly evolved than T. crassicaudata.

Bensley (1903) argued that Thylacoleo was derived from an omnivorous stage in diprotodont development from which it evolved carnivorous adaptations. He points out that in the Dasyuridae the canines become increasingly developed with increasing size and carnivority. In the Phalangeroidea, the smaller most primitive members, the Burramyidae have well developed upper canines. As the omnivorous evolution progresses, these canines become reduced. In Thylacoleo, they are seen to be reduced as are those in Trichosurus or Phalanger.

Similarly, the condition of the enlarged posterior premolars suggests a previous omnivorous or herbivorous function. the excessive enlargement and ungrooved character of these teeth parallels the condition found in the placental carnivores, but is not seen in any marsupicarnivorans.

The piercing function of the median incisors which is apparent in Thylacoleo is unique to Thylacoleo among carnivorous marsupials. However, these teeth do fulfil this function in the insectivorous phalangeroids and dasyurids. Bensley argues that for Thylacoleo to have developed the median incisors in this way then its ancestors must have had dentition similar to the herbivorous phalangeroids to the extent that only the median incisors were left for development as piercing organs.

Bensley thought the molar pattern of *Thylacoleo* to be derived from the bunodont quadrituberculate pattern found in the *Phalangeroidea*.

Woods (1956) has reviewed the fossils of *Thylacoleo* and has concluded that the animal was certainly carnivorous. He has based this conclusion on the shearing modifications which are apparent from examination of the surfaces of wear on the premolars.

Thylacoleo has many features convergent on the placental carnivores including the short rostrum and width of the temporal fassa which imparts a broad sub triangular outline to the skull. Added to this is the typically *Canis*-like carnivore disposition, relative to the temporal fossa of the shearing teeth at occlusion.

Woods pointed out some similarities of *Thylacoleo* to *Phascogale* including the structure of the tympanic bullae and the structure of the stapes.

As to the nature of its diet, Woods concluded that it could not be known from the available fossil evidence, whether *Thylacoleo* was predaceous or a carrion feeder. He thought it unlikely however, that such a large carnivore would have fed exclusively on carrion.

Thylacoleo crassicaudata from the Pliocene Chinchilla Sand is seen to be an older and more primitive species of *Thylacoleo*. It differs from *T. carnifex* in so far as the molars are less reduced in size and number. (Bartholomai 1962).

Gill (1954) has reviewed the ecology and distribution of *Thylacoleo*. He has shown that it extended at least throughout eastern and southern Australia during the Pliocene.

Family Macropodidae

This is the largest family of marsupials consisting of some fifty-six species comprising seventeen genera which are grouped into three sub-families. One of these sub-families is the now extinct Sthenurinae. The sub-families Macropodinae and Potoroinae both have extinct genera. Possibly because of their large size and commonness and possibly because they were frequently preyed upon by the large carnivorous marsupials, they form the greater part of the Australian fossil record.

Ride (1964) and Kirsch (1975) have commented on the confusion which surrounds the taxonomy and phylogeny of the macropods, both extinct and extant.

Seologically, two groups of macropods are evidenced, the Macropodinae and the Potoroinae are distinct from each other. These two groups are more closely related to each other than to any other marsupial families (Kirsch 1968b).

Cytological investigations revealed that the Macropodidae vary in chromosome number from $2n=100$ in Wallabia bicolor to $2n=32$ in Aepyprymnus rufescens. Because of the complexity of the cytological data it will be considered separately in each discussion of sub-families and genera.

It is considered that the phalangeroidea were the ancestral stock from which the Macropodidae arose (Bensley 1903, Tate 1948).

Subfamily Potoroinae

Ride (1964) believes there are three phyletic lines of Macropodidae. First is the Potoroinae, including Hypsiprymnodon, Potorous, Bettongia, Aepyprymnus, Caloprymnus and the extinct Propleopus. Second is the extinct sub-family Sthenurinae with Sthenurus and Procoptodon. Third is the Macropodinae which

includes the remaining extant genera as well as several extinct forms.

The members of Potoroinae share a number of characters including the development of the masseteric canal in confluence with the inferior dental canal (Abbie 1939), and specialisation in several characters of the female urogenital tract beyond the condition seen in the Macropodinae.

Hypsiprymnodon differs from the other members of the Potoroinae in several respects, including the simple alimentary canal (Ride 1964) the narrow contact of the frontal and squamosal bones (Pearson 1950), and the length of the median vaginal sinus (Pearson 1946, 1950). It also differs from the other Potoroinae in the lack of pronounced elongation of the hind foot, in preserving a hallux and in the lack of reduction of the forelimb. (Woods 1960).

Because of these differences, it has been suggested that Hypsiprymnodon should be elevated to sub-family level (Kirsch 1968). However, Woods has argued that the many unique features of the limbs may be adaptive to the rain forest habitat of this genus, there being no advantage to it in developing a staltatory mode of locomotion.

It has been suggested that Hypsiprymnodon is the most primitive member of the Potoroinae, being closer to the macropod main stem of the radiation (Pearson 1950, Woods 1960).

Cytological studies have shown variation of chromosome number and morphology within this sub-family. Hypsiprymnodon has $2n=22$ as do all species so far studied of Bettongia. In Potorous apicalis the chromosome number is $2n=13\sigma^1 12q$ and the sex chromosome complement is $XY_1 Y_2 / XX$ unlike the normal sex chromosome pattern YY/XX found in other genera. Aeprymnus rufescens has $2n=32$ which is the highest chromosome number of any marsupial

(Hayman and Martin 1969). Hayman and Martin consider that $2n=22$ is the primitive chromosome number for the Macropodidae and as yet no workers have been able to explain the occurrence of chromosome numbers greater than $2n=22$.

The XY_1Y_2 / XX sex chromosome system is explained as resulting from an X - autosome fusion and subsequent loss of an acentric fragment. Thus the chromosome number $2n=13o^{12p}$ found in Potorous apicalis is derived from $2n=14$ (Hayman and Martin 1966).

Tate (1948) and Ride (1964) have concluded that the sub-family Potoroinae are an early offshoot from the Macropodinae which are the stem form of the Macropodid radiation.

Reproduction has been studied in Potorous (Pearson 1945, Hughes 1962) and Bettongia (Tyndale Biscoe 1966, 1972). These genera are polyestrous and monotocous. Gestation is almost the same length as but just shorter than the estrous cycle. They have a long period of pouch suckling, usually longer than six months and delayed implantation which is controlled by lactation occurs in these genera. The pseudovaginal birth canal is formed before each parturition. Typically of the macropods, reproduction is specialised in the Potoroinae.

Woods (1960) has referred the extinct genus Propleopus (De Vis 1888) from the late Pliocene (Tedford 1955) to the Potoroinae. He has described it as sharing some characters with Hypsiprymnodon and Bettongia but is closer to Hypsiprymnodon. He does not consider it to be ancestral to any living genus.

The oldest fossils referable to the sub-family Potoroinae are from the Oligocene Ngapakaldi fauna (Stirton et al 1961) have been identified as belonging to the genus Bettongia (Stirton et al 1968). Stirton et al (1968) has suggested that

the Ngapakaldi fauna may contain another species of potoroine but have as yet not described it.

Turnbull and Lundelius (1970) have recorded several potoroines from the Pliocene Hamilton fauna. Ride (1964) has re-examined one of these known as the Grange Burn Potoroo. However, because of the fragmentary nature of the fossil he was unable to decide whether it should be included in *Propleopus* on the basis of its size or whether it should be regarded as a giant *Potorous*.

Bartholemai (1972) records the finding of a small species of *Propleopus* from possibly Pliocene sediments of New South Wales.

The Genera *Potorous*, *Aepyrynus* and *Bettongia* have been found in Pliestocene or recent deposits and the material is close to or identical to living forms (Marshall 1973, Merrilees 1973, Stirton et al 1968).

Bartholomai (1972) has devised a phylogeny for the Potoroinae based on known fossil records, Fig. 14.

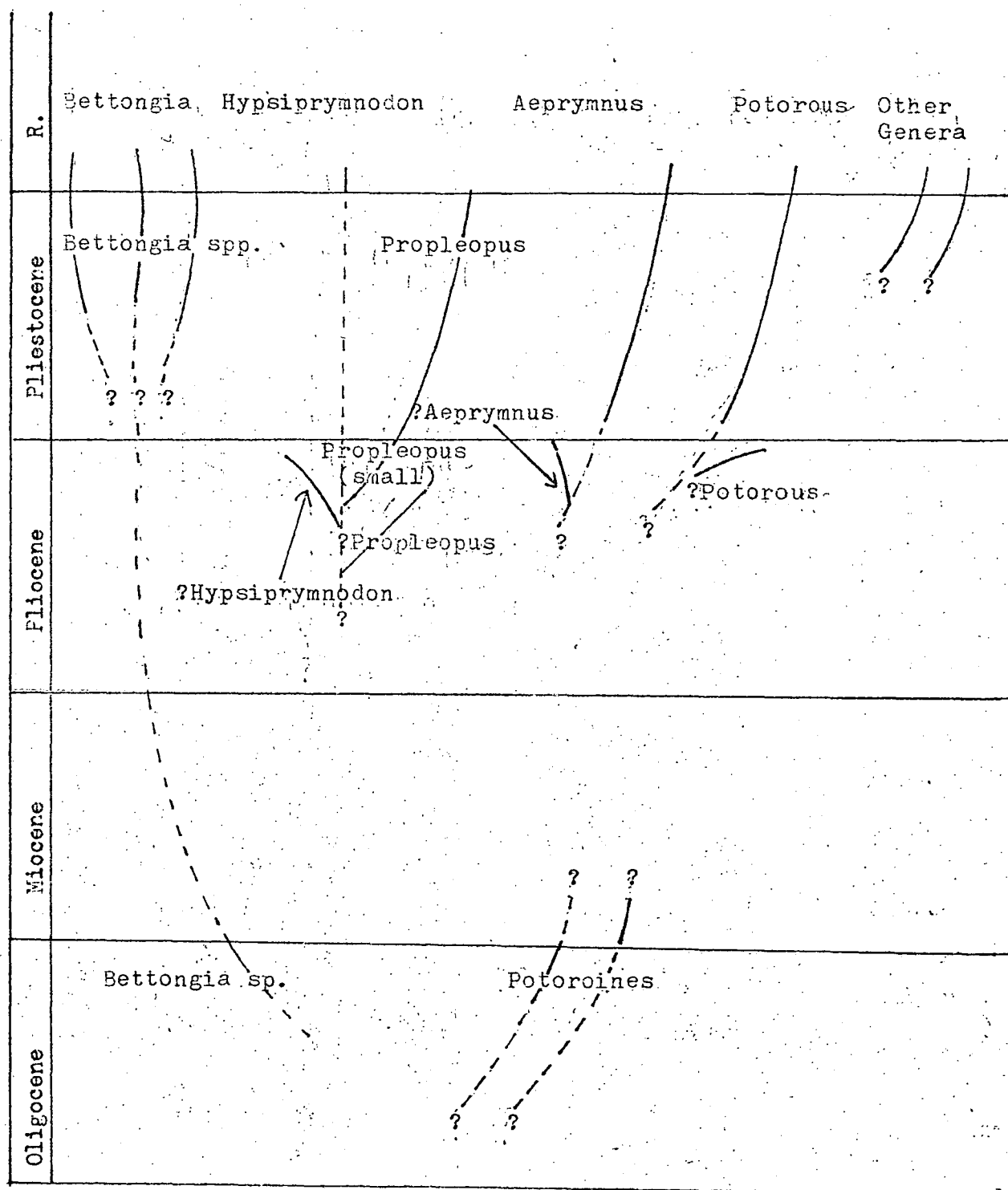


Fig. 14 Phylogenetic Relationships within the Potoroinae.
(After Bartholomai 1972).

Sub-family Sthenurinae

A more recent offshoot from the main macropodid line is the now extinct sub-family Sthenurinae. This sub-family is remarkable for its late derivation, rapid radiation, convergent tendencies and specialisation within an already widely diversified family (Bartholomai 1972).

The affinities of the Sthenurinae with the Macropodinae can be seen from examination of skull structure, dentition and hind feet. In these structures there are many features which are shared by the two groups (Tedford 1966).

Woodburne (1967b) has suggested that the species Hadronomas puckeridgei from the Alcoota formation may be close to the lineage leading towards Sthenurus. Bartholomai (1972) has concluded that it is unlikely that the Sthenurinae arose much before the late Miocene and the greatest radiation is found in the Pliocene.

Tedford (1966) concluded that the macropodine radiation took place in later Cenozoic times in response to spreading savanna and grassland habitats. It is possible that Sthenurus, a product of this adaptive radiation may have been one of the earliest groups to successfully exploit the developing savannas and grasslands.

The sthenurine radiation took place along two main morphological lines. The first of these, comprising the dolicocephalic sub-genus Sthenurus, was a continuation of the primitive grazing adaptation seen in early Sthenurinae and Macropodinae. The other line actually consists of two phyletic lines which are convergently brachycephalic and adapted to a browsing savanna and woodland habit. The brachycephalic types are included in the genus Sthenurus (Simosthenurus) and the

genus *Procoptodon*.

The skull of the brachycephalic species is short, wide and deep, the occipital condyles are elevated well above the palatal plane. The zygomatic process of the squamosal is vertically deep and the maxillary and jugal bones are jointly produced forming a strong downwards directed masseteric process.

In the dolicephalic species the skull is closer to the skulls of the Macropodinae, being more elongate than the skulls of the brachycephalic group, particularly in the pre-orbital regions. The skull is narrower and shallower with the occipital condyles only moderately elevated above the plane of the palate. The masseteric process of the zygoma is formed mostly by the maxillary (Tedford 1966 p. 8).

Although *Sthenurus* (*Simosthenurus*) resembles *Procoptodon* in gross features of the skull and jaws there are fundamental dental differences. Thus *Simosthenurus* and *Sthenurus* share characters such as the late eruption of the permanent premolars compared with *Procoptodon* and the relative size and shape of the incisors. In *Procoptodon* the trend towards the development of monodactylism is advanced beyond the condition seen in the sub-genera of *Sthenurus* (Bartholomai 1963, Tedford 1967b).

Tedford (1966) has suggested that both genera of browsing *Sthenurines* evolved in parallel during late Cenozoic time and the extent of the dental differences apparent by the Pliestocene suggests that they had diverged from a common *sthenurine* ancestor by the Pliocene. He has further concluded that the double invasion of the browsing adaptive zone by the large *sthenurines* indicates an absence of other large browsing

marsupials. It is possible that competition between the sthenurines and the rapidly evolving macropodines may have pressured the evolution of adaptations to diets of plants, leaves and bark rather than herbs and grasses.

The massive size of the Pliestocene Sthenurinae is an adaptation to its browsing habit. However, the Pliestocene was a period marked by gigantism in many mammal orders throughout the world (Keast 1972).

Tertiary fossil deposits containing sthenurine remains are uncommon. Three species of *Sthenurus* have been described by Bartholomai (1963) from the Chinchilla sand fauna. Stirton et al (1961) have recorded a sthenurine from the Palankarinna fauna.

Sthenurine fossils are relatively common in Pliestocene deposits (Bartholomai 1963, Tedford 1966, Merrilees 1965, 1967). The geographical locations of deposits containing fossils of Sthenurinae show that the sub-family was widely distributed. No fossils have been recovered as yet from Western Australia.

The most recent known fossils of *Sthenurus* are from the Lake Menindee deposits of New South Wales, which have been dated at $26,300 \pm 1500$ years BP (Hubbs et al 1962). The most recent fossils of *Procoptodon* are from the Lake Colongulac deposits of Victoria and have been dated at $13,725 \pm 350$ years BP. (Gill 1955).

A phylogeny for the Sthenurinae has been suggested by Bartholomai (1972) and is presented in Fig. 15

Summary

The Sthenurinae, an extinct sub-family which had a wide radiation in the Pliestocene was derived from macropod ancestors probably during the Miocene.

The sthenurines were primitively grazing herbivores, *Sthenurus* (*Sthenurus*) but evolved two parallel groups of browsers, *Sthenurus* (*Simosthenurus*) and *Procoptodon*.

The evolution of browsing forms may have occurred in response to competition with the grazing *Macropodinae*. In *Procoptodon*, adaptations to a cursorial mode of locomotion are seen in the development of monodactylism.

Sthenurinae is thought from the fossil record, to have become extinct in recent time.

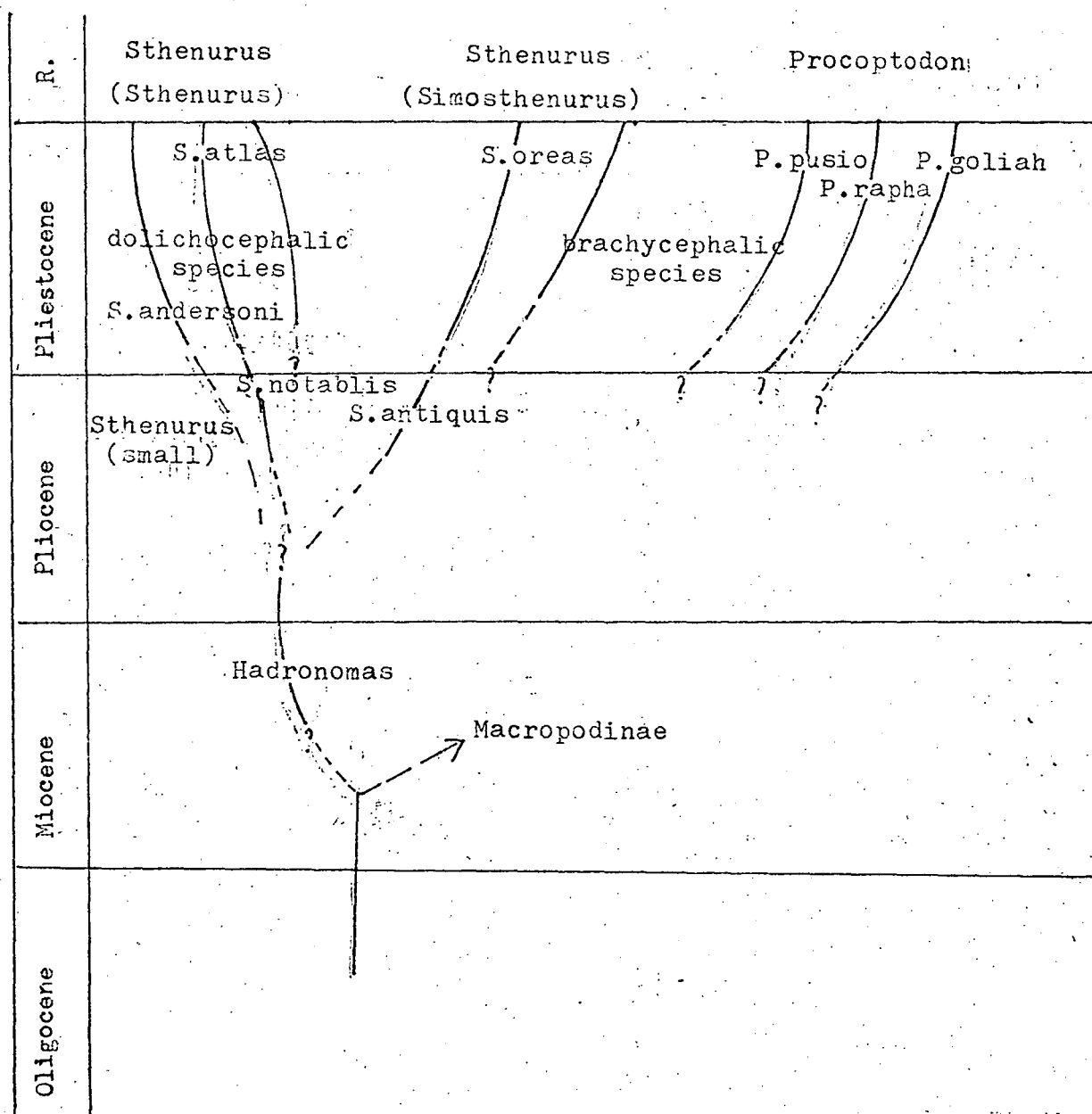


Fig. 15 Phylogenetic Relationships of the Sthenurinae Based on Fossil Data (after Bartholomai 1972).

Sub-family Macropodinae

The Macropodinae is the largest and most specialised marsupial group. It is a terrestrial derivation from phalangeroid stock which involved the evolution of a grazing herbivorous, saltatory habit (Bensley 1903, Marshall 1972).

Ride (1962, 1964) and Bartholemai (1972) have discussed the problems associated with phylogeny of the macropodines both extant and extinct.

The oldest fossils which have been referred to this sub-family are from the Miocene Kutjamarpu deposits. (Stirton et al 1968) and Bartholemai (1972) have concluded that its ancestry must be pre-Oligocene. It is during the Pliocene and Pliestocene (Stirton 1955, 1957, Stirton et al 1961, 1968, Bartholemai 1966, 1967, 1969, Tedford 1967a, 1967b, Woodburne 1967b) however, that the extensive radiation of the Macropodinae took place, probably as was the case with the Sthenurinae, in response to expanding grasslands and savanna (Keast 1959).

The karyotypes of the Macropodinae are variable and in *Petrogale* which is found in isolated populations the chromosome numbers range from $n=18$ to $n=22$. In species with the same chromosome number, there are marked differences in chromosome morphology (Hayman and Martin 1974).

The species of *Lagorchestes* are also variable (Hayman and Martin 1969).

Many of the species of the Macropodinae exhibit a chromosome number of $2n=16$ with similar chromosome morphology. (Hayman and Martin 1969). Calaby (1966) has suggested that these species should all be referred to the genus *Macropus*. The red kangaroo with $2n=20$, which was previously thought to be separate from the genus *macropus*, has been shown (Sharman and

Calaby unpublished in Kirsch 1975) to be cytologically closer to M. antilopus, M. bernadus and M. robustus; than to any other members of macropus. For this reason, it is now included in this genus as M. rufus.

The genus Macropus has fourteen species and there are generally different environmental habitats. Thus the large M. rufus is a plains dwelling type of the central region while M. parma is a small species inhabiting the dense undergrowth of rain forest.

Wallabia bicolor which is cytologically distinct from all other Macropodine with $2n=10q \quad 11o$ (Sharman 1961) has been placed in the monotypic genus Wallabia (Calaby 1966). It differs in breeding biology and behaviour from all other kangaroos (Sharman et al and Poole 1966). It is unique among the Macropodinae in its possession of a massive permanent premolar and in molar features such as low links and low lophs which are reminiscent of the Pliocene and Plietocene Protomodon (Kirsch 1975).

Reproduction in the Macropodinae is sophisticated. They are all monotocous and polyestrous. Gestation is just shorter than one estrous cycle in some Macropus, Setonix and Thylogale. In Wallabia bicolor it is thought (Sharman et al 1966) that gestation exceeds the length of an estrous cycle. In the above types, delayed implantation occurs which is controlled by lactation. However, in M. kanguru the gestation period exceeds the length of an estrous cycle but lactation controlled delayed implantation does not occur.

In parous females of all Macropodinae except for Lagostrophus and M. kanguru, the median vaginal canal is permanently formed.

Tate (1948) divided the Macropodinae into three phyletic groups on the basis of development of the canines. His phylogeny with modifications based on recent neontological data is shown in Fig. 16.

The fossil evidence for the evolution of the Macropodinae has been summarised by Bartholomai (1972) and his phylogeny based on fossil data is presented in Fig. 17.

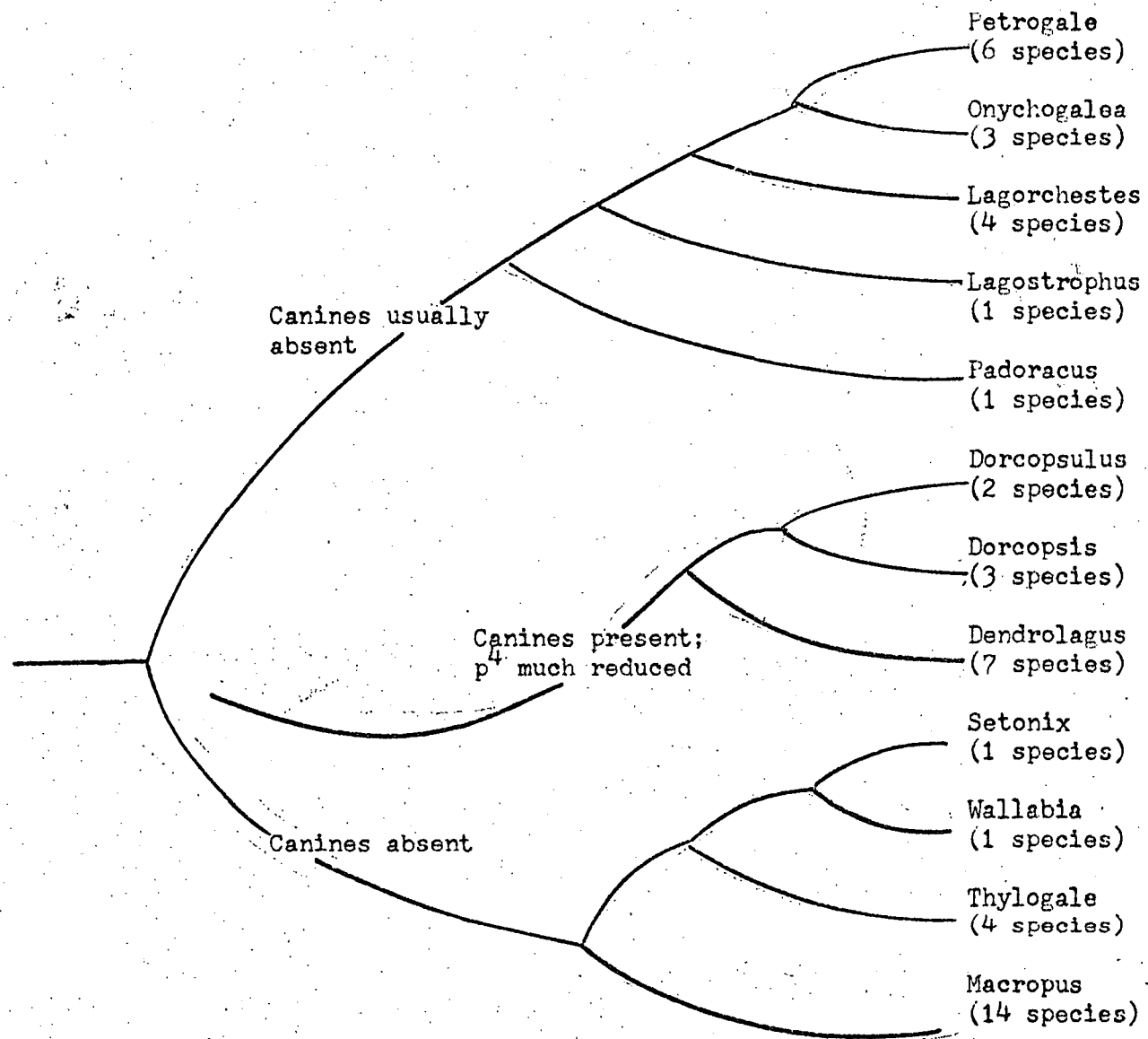


Fig. 16

Phylogeny of the Macropodinae (modified after

Tate 1948, Calaby 1966, Kirsch 1975).

SUPERFAMILY VOMBATOIDEA

Kirsch (1968b) proposed the superfamily Vombatoidea to include the wombats and the koala which he found to be serologically closer to each other than to any other marsupials.

Vombatoidea contains two families, the Phascolarctidae which contains one extant species, Phascolarctos cinerus and the extinct Koalemus vombatidae and the Vombatidae with two extant genera Vombatus and Lasiorhinus and two extinct genera Phascolonus and Phasolomys.

The origins of the Vombatidae are unknown although the Miocene fossil Perikoala palankarina (Stirton 1957, Stirton et al. 1961) is described as resembling both Trichosurus vulpecula, a phalangerid, and Phascolarctos.

The relationship between the wombats and the koala is evidenced by comparisons of myology (Sonntag 1922), reproductive physiology (Hill 1949) and spermatozoa (Hughes 1965). There are however, cytological differences with a chromosome number of $2n=14$ in the Vombatidae, (Sharman 1961) and a chromosome number $2n=16$ in the Phascolarctidae with differences in chromosome morphology (Sharman 1961).

In the Vombatoidea there arise two instances of deviation from the usual marsupial rib number of thirteen pairs of ribs. Vombatus has fifteen pairs of ribs and Phascolarctos has eleven pairs (Stephenson 1967).

Family Vombatidae

There are presently two extant genera of Vombatidae, Vombatus and Lasiorhinus. The dental pattern of the Vombatidae is aberrant in having open rooted teeth which grow continuously through life. (Stephenson 1967). In this respect they resemble

the incisor teeth of rodents and the cheek teeth of the lagomorphs. The wombats are large animals with short strong limbs and long chisel-shaped claws. The skull is massive and flattened and the bullae are small. The muscular limbs are adaptations to the burrowing habit of wombats as is the flattened skull. They are fossorial, herbivorous marsupials and the atypical dentition found in the wombats is an adaptation to this mode of life.

The systematics of the fossil wombats confused (Ride 1964, Stephenson 1964, 1966, Merrilees 1967, Ride 1967). However, it is agreed that there were at least three species of giant Pliestocene wombats, Phascolonus gigas, Phasolomys magnus and Phascolomys medius, (Owen 1872). The giant wombats appear to be more closely related to the extant Lasiorhinus genus than to Vombatus. Stephenson (1966) has suggested that the two species of Phascolomys should be transferred to either Lasiorhinus or Phascolonus.

At present Vombatus occurs in eastern Australia from southern Queensland to southeastern South Australia and in Tasmania and some Bass Strait Islands. It inhabits wet and dry sclerophyll forests and especially rocky country.

Lasiorhinus is found in savannah woodland areas and grasslands in southern South Australia, eastern West Australia, eastern Queensland and the Riverina area of New South Wales (Ride 1970).

Fossil evidence indicates that the wombats were more widespread in the past (Stephenson 1966).

Family Phascolarctidae

This monotypic family contains the highly specialised, arboreal koala, Phascolarctos cinerus.

As well as the neontological data which was mentioned on p. 105, fossil evidence (Bartholomai 1968) supports the conclusion that Phascolarctidae is most closely related to Vombatidae.

The similarities of the selonodont dentition in Phascolarctos and some Phalangeridae is now thought to be a case of parallel evolution as in both types, the diet is similar (Ride 1964).

The koala is presently restricted to dry sebrophyll woodlands of eastern Australia (Ride 1970). It is unknown from New Guinea or Tasmania.

Family Diprotodontidae

The extinct family Diprotodontidae has been reviewed by Stirton et al (1967).

There are some cranial characters held in common with the Vombatidae such as the exclusion by the squamosal of the alisphenoid from the auditory region and the presence of open rooted teeth (Stirton 1967(a)). The early Miocene specimens which are the oldest known, show no direct evidence that the teeth have been derived from ancestors with tribosphenic molars. Thus it is concluded that the Diprotodontidae were well established by the Miocene (Stirton et al 1967).

The diprotodontids were quadrupedal, herbivorous marsupials, some of which, e.g. Zygomaturinae achieved great size.

Stirton et al (1967) have described four subfamilies of diprotodontids, Palorchestinae, Nototheriinae, Zygomaturinae and Diprotodontinae.

The oldest fossils, from the Ngapakaldi fauna, which are early Miocene or possibly late Oligocene, contain a form Ngapakadia, which is thought to be the most generalised diprotodontid and retains alveoli for vestigial upper canines which are absent in other Diprotodontidae. It is possible that they exhibit some ancestral features of the Diprotodontidae and that the Palorchestinae in which they are included are ancestral to later diprotodontid groups. The Palorchestinae are small marsupials in comparison with the later diprotodontids.

A phylogeny of the Diprotodontidae based on paleontological evidence is presented in Stirton et al (1967); see fig. 18

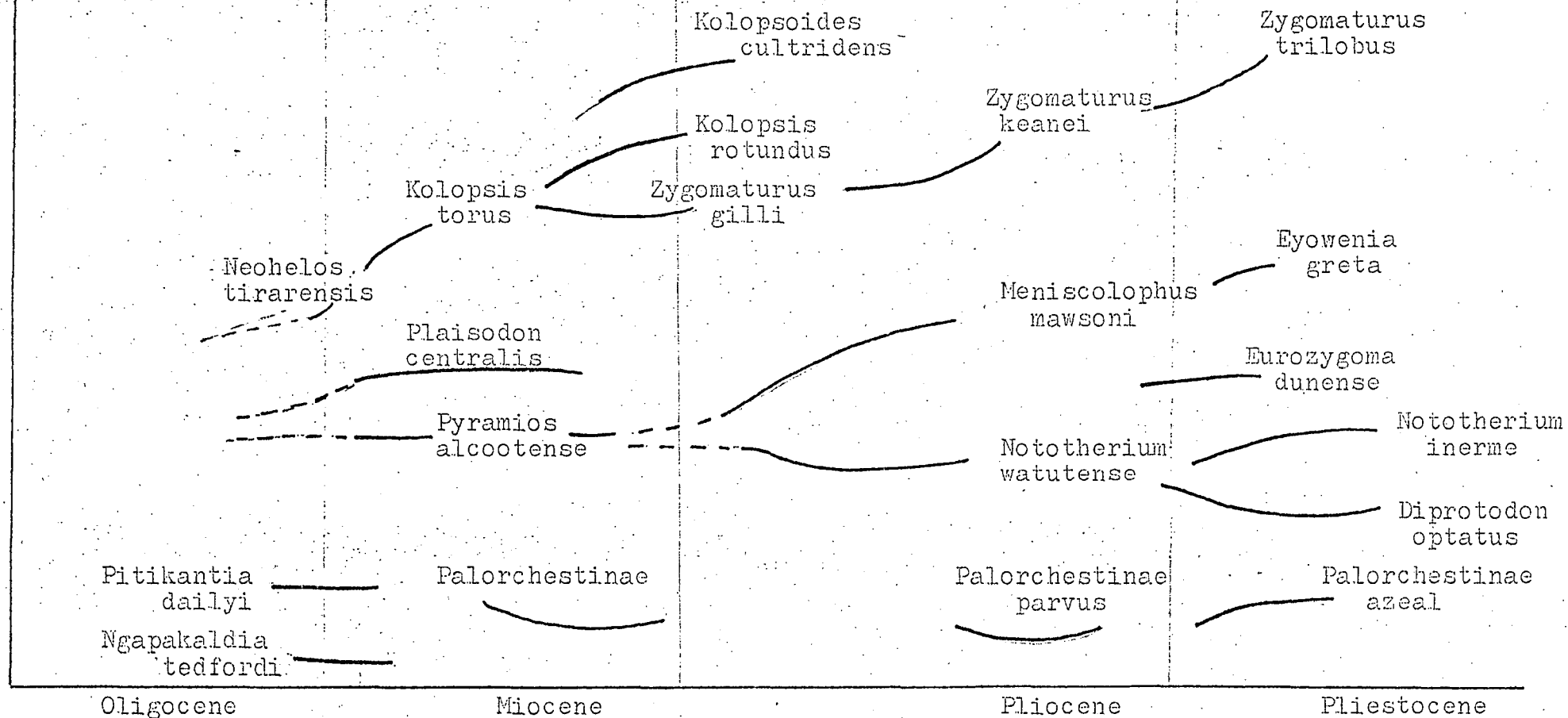


Fig. 18' Phylogeny of the Diprotodontidae (after Stirton et al 1967).

SUPERFAMILY TARSIPOIDEAFamily Tarsipidae

This monotypic family contains the honey possum Tarsipis spenceri. It is the most divergent diprotodont marsupial, both morphologically and serologically (Kirsch 1975). Cytologically, it most closely resembles Trichosurus (Hayman and Martin 1969).

It is a highly specialised nectar and pollen feeder with a long tube-like mouth and a tongue which is brushed at the end. It possibly supplements the pollen-nectar diet with small insects which occur on the food blossoms (Ride 1970).

SUPERFAMILY NOTORYCTOIDEAFamily Notoryctidae

This monotypic family contains the marsupial mole, Notoryctes typhlops which converges upon the placental moles, Chrysochloridae and Talpidae. It is highly specialised in dentition, skull structure and limb structure and its relationships are obscure. Bensley (1903) included it with the Peramelids on the basis of foot structure. Wood Jones (1923) and Simpson (1945) related it to the dasyurids. Van der Klaauw (1931) pointed out that the development of the tympanic in Notoryctes agrees more closely with the Diprotodonta than the Marsupicarnivora.

Cytological studies (Calaby et al 1974) show that the chromosomes bear a strong resemblance to Petaurus breviceps; Phalangeroidea.

Serologically (Kirsch 1975 unpublished) Notoryctes appears to have dasyuroid - perameloid affinities.

BIBLIOGRAPHY

- Abbie, A.A., 1941: Marsupials and the evolution of mammals. Aust. J. Sci. 4: 77-92.
- Anon.: 1966: A relict marsupial. Nature 212:225
- Bakker, R.I., 1975: Dinosaur Renaissance. Sci. Am. 232: 58-78.
- Bartholemai, A., 1962: A new species of Thylaeoleo and notes on some caudal vertebrae of Palorehestes azael. Mem Qd. Mus 14: 33-40.
- Bartholemai, A., 1963: Revision of the extinct macropodid genus Sthenurus Owen in Queensland. Mem. Qd. Mus. 14: 51-76.
- Bartholemai, A., 1966: The Type Specimens of some of De Vis Species of fossil Macropodidae. Mem Qd. Mus. 14: 115-126.
- Bartholemai, A., 1967: Troposodon a new genus of fossil Macropodinae (Marsupialia). Mem. Qd. Mus. 15: (1): 21-34.
- Bartholemai, A., 1968: A new fossil Koala from Queensland and a reassessment of the Taxonomic position of the problematical species, Koalemus ignens De Vis. Mem. Qd. Mus. 15(2): 65-72.
- Bartholemai, A., 1970: The Extinct Genus Procoptodon Owen (Marsupialia: Macropodidae) in Queensland. Mem. Qd. Mus. 15(4): 213-234.
- Bartholemai, A., 1971(a): Morphology and variation of the cheek teeth in Macropus giganteus Shaw and Macropus agilis (Gould). Mem. Qd. Mus. 16: 1-18.
- Bartholemai, A., 1971(b): Dasyurus dunmalli, a new species of fossil Marsupial (Dasyuridae) in the Upper Cainozoic deposits of Queensland. Mem. Qd. Mus. 16: 19-26.
- Bartholemai, A., 1972: Aspects of the Evolution of the Australian Marsupial. Proc. Roy. Soc. Qd. 82: 5-28.
- Bartholemai, A., 1975: The genus Macropus Shaw (Marsupialia: Macropodidae) in the Upper Cainozoic deposits of Queensland. Mem. Qd. Mus. 17: (2). 195-236.
- Bensley, B.A., 1903: On the Evolution of the Australian Marsupialia. Trans. Linn. Soc. Lond. Ser. 2. (Zool.). Vol. IX: 13-217.
- Berkovitz, B.K.B., 1967: The Order of cusp development on the molar teeth of Setonix brachyurus (Macropodidae, Marsupialia). J. Roy. Soc. West. Aust. 50: 41-48.

- Biggers, J.D., H.I. Fritz, W.C.D. Hare and R.A. McFeely, 1965: Chromosomes of American Marsupials. Science V.118: P. 16802-1603.
- Biggers, J.D., 1966: Reproduction in male marsupials. In Zool. Soc. Lond. Symposia 15. (Ed. W. Rowlands) pp. 251-280. Lond. Academic Press.
- Broom, R., 1896: On a small fossil marsupial with large grooved premolars. Proc. Linn. Soc. N.S.W. (2) 10: 563-567.
- Broom, R., 1896(a): On a small fossil marsupial allied to Petaurus. Proc. Linn. Soc. N.S.W. (2) 10: 568-570.
- Broom, R., 1896(b): Report on a abone breccia deposit near the Wombeyan Caves, N.S.W., with descriptions of some new species of marsupials. Proc. Linn Soc. N.S.W. 21: 48-61.
- Broom, R., 1898: On the affinities and habits of Thylacoleo. Proc. Linn. Soc. N.S.W. 23: 57-74.
- Butler, P.M. and Z. Kielan-Jaworowska, 1973: Is Deltatheridium a Marsupial? Nature 245: 105-106.
- Calaby, J.H., 1966: Mammals of the upper Richmond and Clarence Rivers, New South Wales. C.S.I.R.O. Division of Wildlife Research Technical Paper No. 10: 1-55.
- Calaby, J.H., L.K. Corbett, G.B. Sharman and P.G. Johnston, 1974: The Chromosomes and Systematic Position of the Marsupial Mole, Notoryctes typhlops. Aust. J. Biol. Sci. 27: 529-32.
- Clark, M.J., 1966: Pregnancy in the lactating Pigmy Possum Cercartetus concinnus. Aust. J. Zool. 15: 673-83.
- Clemens, W.A., 1968: Origin and Early Evolution of Marsupials. Evolution 22: 1-18.
- Clemens, W.A., 1971: Mammalian evolution in the Cretaceous. In Early Mammals (Kermack and Kermack eds.) p. 165-180. London Academic Press.
- Colbert, E.H. 1971: Tetrapods and Continents. Quart. Rev. Biol. 50: 21-25.
- Colbert E.H., D. Merrilees, 1967: Cretaceous dinosaur footprints from Western Australia. J. Roy. Soc. West. Aust. 50: 21-25.
- Cranwell, L.M., 1964: Nothofagus: living and fossil. In J.L. Gressett, ed. Pacific Basin Biogeography, p. 387-400. Bishop Museum Press, Honolulu.
- Crowcroft, P., 1967: Studies on the Hairy nosed Wombat Lasiorchinus latifrons (Owen 1845) 1 Measurements and Taxonomy. Rec. S. Aust. Mus. 15: 383-398.

- Darlington, P.J., 1957: Zoogeography: The Geographical Distribution of Animals. John Wiley, London.
- Darlington, P.J., 1965: Biogeography of the Southern End of the World. Howard Univ. Press, Cambridge.
- Dawson, T.J., and A.J. Hulbert, 1970: Standard metabolism, body temperature, and surface areas of Australian marsupials. Am. J. Physiol. 218: 1233-38.
- De Vis, C.W., 1888: On an extinct genus of the Marsupials allied to Hypsprymnodon. Proc. Linn. Soc. N.S.W. 3: 5-8.
- Elliot, D.H., E.H. Colbert, W.J. Breid, J.A. Jensen and J.S. Powell, 1970: Triassic Tetrapods from Antarctica: evidence for continental drift. Science 169: 1197-1201.
- Enders, R.K., 1966: Attachment, nursing and survival of young in some didelphids. Symp. zool. soc. lond. 15: 195-203
- Fitzpatrick, K.T. and C.H. Summerson, 1971: Some observations on Electron micrographs of quartz and sand grains. Ohio. J. Sci. 71: 106-119.
- Fox, R.C., 1971: Marsupial Mammals from the early Companion Milk River Formation, Alberta, Canada. In Early Mammals (Kermack and Kermack eds.) p. 145-164. London, Academic Press Inc. (London) Ltd.,
- Gill, E.D., 1953: Australian Tertiary Marsupials. Aust. J. Sci. V. 16: p. 106-108.
- Gill, E.D., 1954: Ecology and distribution of the extinct giant marsupial Thylacoleo. Vict. Nat. Melb. 71: 18-35.
- Gill, E.D., 1955: Radio carbon dates for Australian archeological and geological samples. Aust. J. Sci. 18: 49-52.
- Gill, E.D., 1957: The stratigraphic occurrence and paleoecology of some Australian Tertiary Marsupials. Mem. Vict. Nat. Mus. 21: 135-199.
- Gill, E.D., 1962: Cainozoic pp. 233-253 in "The Geology of Tasmania" (Eds. A. Spry and M.R. Banks) J. Geol. Soc. Aust. 9(2): x, 107-362.
- Gunson, M.M., G.B. Sharman and J.A. Thomson, 1968: The Affinities of Barramys (Marsupialia: Phalangerioidea) as revealed by a study of its Chromosomes. Aust. J. Sci. 31: 40-41.
- Hayman, D.L. and P.G. Martin, 1965: Sex Chromosome mosaicism in the marsupial genera Isodon and Perameles. Genetics 52: 1201-6.
- Hayman, D.L. and P.G. Martin, 1969: Cytogenetics of marsupials. In comparative Mammalian Genetics. An International Conference at Dartmouth Medical School, Hanover, New Hampshire, July 29-Aug. 2. New York Springer-Verlag pp. 191-217.

- Hayman, D.L., P.G. Martin and P.F. Waller, 1969: Parallel mosaicism of supernumary chromosomes and sex chromosomes in Echymipera kalabu (Marsupialia) Chromosoma (Berl). 27: 371-80.
- Hayman, D.L., J.A.W. Kirsch, P.G. Martin and P.F. Waller, 1971: Chromosomal and Serological Studies of the Caenolestidae and their Implications for Marsupial Evolution. Nature 231: 194-195.
- Hecht, M.K., 1963: A revaluation of the early history of the frogs pt. II. Syst. Zool. 12: 20-35.
- Hershkovitz, P., 1971: The Recent Mammals of the Neotropical Region: A Zoogeographic and Ecological Review. In Mammals and Southern Continents. Keast A. F.C. Erh. and B. Glons (eds.). New York. State University of New York Press.
- Hill, J.P., 1949: The Allantoic Placenta of Perameles. Proc. Linn. Soc. Lond. 161, 3-7.
- Hopson, J.A., 1971: Part Canine replacement in the gomphodont cynodont Diademodon. In Early Mammals. Kermack, D.M. and K.A. Kermack (Eds.) London Academic Press.
- Hubbs, C.L., Bien, C.S. and Seuss, H.E., 1962: La Jolla natural radiocarbon measurements II. Radiocarbon 4: 204-238.
- Hughes, R.L., 1965: Comparative morphology of spermatozoa from five marsupial families. Aust. J. Zool. 13: 533-43.
- Hughes, R.L., 1974: Morphological Studies on Implantation in Marsupials. J. Reprod. Fert. 39, 173-186.
- Huxley, T.H., 1880: On the Application of the laws of evolution to the arrangement of the Vertebrate and more particularly of the Mammalia. Proc. Zool. Soc. Lond. 1880: 649-62.
- Iredale, T. and E. Le G. Troughton, 1934: A check list of the mammals recorded from Australia. The Australian Museum, Sydney, Memoir VI.
- Jardine, N., and D. McKenzie, 1972: Continental Drift and the Dispersal and Evolution of Organisms. Nature 235: 20-24.
- Kean, R.I., 1961: The evolution of marsupial reproduction. Tech. Pap. For. Res. Inst. N.Z. No. 35.
- Kean, R.I., R.G. Mamyatt and A.L.K. Carroll, 1964: The female Urogenital System of Trichosurus Vulpecula (Marsupialia) Aust. J. Zool. 12: 18-
- Keast, A., 1959: Vertebrate Speciation in Australia: Some Comparisons between Birds, Marsupials and Reptiles. In the Evolution of Living Organisms, G.W. Leeper, ed. Melb. Univ. Press.

- Keast, A., 1972: Australian Mammals: Zoogeography and Evolution. In Evolution Mammals Southern Continents, Keast, A., F.C. Erk and B. Glass (Eds.) New York. State University of New York Press.
- Kermack, K.A., 1963: The cranial structure of the Tricodonts. Phil. Trans. R. Soc. (Ser. B) 246: 83-103.
- Kermack, K.A., 1967: The interrelations of early mammals, J. Linn. Soc. (Zool.) 47: 241-249.
- Kermack, K.A., P.M. Lees and F. Mussett, 1965: Aegialodon dawsoni a new trituberculo-sectorial tooth from the Lower Wealdon. Proc. R. Soc. Ser. B. 162: 535-554.
- Kermack, K.A. and E. Mussett, 1958: The jaw articulation of the Docodonta and the classification of Mesozoic mammals Proc. Roy. Soc. Lond. B. 148: 204-215.
- Kielan-Jaworowska, Z., 1975: Possible occurrence of marsupial bones in Cretaceous eutherian mammals. Nature 255: 698-699.
- Kirsch, J.A.W., 1968(a): The Serological Affinities of Burramys and Related Possums (Marsupialia: Phalangeroidea). Aust. J. Sci. 31: 43-45.
- Kirsch, J.A.W., 1968(b): Prodrum of the Comparative Serology of Marsupialia. Nature 217: 418-420.
- Kirsch, J.A.W., (In Press), 1976: Biology of Marsupials V.I. Acacad. Press.
- Kirsch, J.A.W. and W.E. Poole, 1967: Serological Evidence for Speciation in the Grey Kangaroo, Macropus giganteus Shaw 1790 (Marsupialia: Macropodida). Nature 215: 1097-8.
- Kirsch, J.A.W., and M.D. Murray, 1969: A scheme for the identification of the blood of Australasian Marsupials. Aust. J. Zool. 17: 799-816.
- Kitts, D.B., 1974: Paleontology and Evolutionary Theory. Evolution 28. 458-472.
- Klaauw, C.J. van der, 1931: The auditory bulla ; in some fossil mammals with a general introduction to this region of the skull. Bull. Amer. Mus. Nat. Hist. 62: 1-352.
- Kurten, B., 1967: Continental drift and the paleogeography of reptiles and mammals. Comment Biol. Soc. Sci. Fennica 31(1): 1-8.
- Kurten, B., 1969: Continental drift and Evolution. Sci. Am. 220(3): 54-64.
- Lillegraven, J.A., 1969: Latest Cretaceous mammals of Upper part of Edmonton formation of Alberta, Canada, and review of marsupial - placental dichotomy in mammalian evolution. Univ. Kansas. Paleont. Contrib. Art. 50. (Vert 12): 1-122.

- Longman, H.A., 1925: Fossil Marsupials from Queensland. Mem. Qd. Mus. 8: 109-10.
- McKenna, M.C., 1970: The origin and early differentiation of Therian Mammals. Ann. N.Y. Acad. Sci. 167: 217-240.
- Mackenzie, W.C., 1918: The Liver, Spleen, Pancreas, Peritoneal Relations and Biliary System in Monotremes and Marsupials. Critchley Parker Australia 1918.
- Macintyre, G.T., 1972: The Triscutate Petrosal Pattern of Mammals. In Evolutionary Biology V. 6. p. 275-303. (Dobzhansky, T., M.K. Hecht and W.C. Steere, eds.) New York, Appleton Century Crafts.
- Margolis, S.V., and J.P. Kennett, 1970: Antarctic glaciation during the Tertiary recorded in sub-Antarctic deep sea areas. Science 170: 1085-87.
- Marshall, L.G., 1972: Evolution of the peramelid tarsus. Proc. Roy. Soc. Vict. 85: 51-60.
- Marshall, L.G., 1973: Fossil vertebrate faunas from the Lake Victoria region, S.W. New South Wales, Aust. Mem. Nat. Mus. Vict. 34: 151-172.
- Martin, P.G., 1970: The Darwin Rise Hypothesis of the Biogeographical Dispersal of Marsupials. Nature 225. pp. 197-198.
- Martin, P.G. and D.L. Hayman, 1967: Quantitative Comparisons Between the Karyotypes of Australian Marsupials from Three different Superfamilies. Chromosome 20: 290-310
- Mascon, L.R., V.M. Sarich and A.C. Wilson, 1975: Continental drift and the use of albumen as an evolutionary clock. Nature 255pp. 397-341.
- Merrilees, D., 1965: Two species of the extinct genus *Sthenurus* Owen (Marsupialia, Macropodidae) from south eastern Australia, including *Sthenurus gilli* sp. nov. Roy. Soc. West. Aust. 48: 22-32.
- Merrilees, D., 1967a: Cranial and Mandibular Characters of Modern Mainland Wombats (Marsupialia, Vombatidae) from a Paleontological viewpoint, and their bearing on the fossils called *Phascolonus parvus* (Owen 1872) Rec. S. Aust. Mus. 15: 399-418.
- Merrilees, D., 1967b: Southwestern Australian occurrence of *Sthenurus* (Marsupialia, Macropodidae) including *Sthenurus brownei* sp. nov. J. Roy. Soc. West. Aust. 50: 65-79.
- Merrilees, D., 1967c: Fossil Bandicoots (Marsupialia, Peramelidae) from Mammoth Cave, Western Australia, and their climatic implications. J. Roy. Soc. West. Aust. 50: 121-128.

- Merrilees, D., 1967(d): Fossiliferous deposits at Lake Tandau, N.S.W., Australia. Mem. Nat. Mus. Vict. 34: 177-182.
- Mills, J.R.E., 1971: The dentition of Morganucodon. In Early Mammals. Kermack, D.M. and K.A. Kermack, eds. p. 29-63. Academic Press Lond.
- Newsome, A.D. and K.A. Rochow, 1964: Vertebrate fossils from Tertiary sediments of Central Australia. Aust. J. Sci. 26(11): 352.
- Owen, R., 1872: On the fossil mammals of Australia. VI Genus Phascolomys Geoffr. Phil. Trans. R. Soc. 162: 173-96.
- Partridge, J., 1967: A 3,300 year old Thylacine (Marsupialia, Thylacinidae) from the Nullabor Plain, Western Australia. J. Roy. Soc. West. Aust. 50: 57-59.
- Patterson, B., 1967: Infra Class Metatheria Superorder Marsupialia. In the Fossil Record. Part II Mammalia p. 763-783. Geol. Soc. Lond.
- Patterson, B. and A. Pascual, 1968: Evolution of mammals on Southern Continents. The fossil fauna of South America. Quart. Rev. Biol. 43: 409-451.
- Patterson, B. and R. Pascual, 1972: The fossil Mammal Fauna of South America: In Evolution Mammals and Southern Continents, Keast, A., F.C. Erk and B. Glass (Eds.) New York. Stat University of New York Press.
- Pearson, J., 1950; The Relationships of the Potoroidae to the Macropodidae (Marsupialia) Pap. Roy. Soc. Tas. 1949: 211-229.
- Pilton, P.E. and G.B. Sharman, : Reproduction in the Marsupial Trichosurus vulpecula. J. Endocrinology V.25 P. 119-36.
- Plane, M.D., 1967(a): Two new diprotodontids from the Pliocene Otibanda Formation, New Guinea. Bull. Bur. Min. Res. No. 85: 105-128.
- Plane, M.D., 1967(b): The stratigraphy and vertebrate fauna of the Otibanda Formation, New Guinea. Bull. Bur. Min. Res. 86p. 1-64.
- Plane, M. and C.G. Gatehouse, 1968: A new vertebrate fauna from the Tertiary of Northern Australia. Aust. J. Sci. 30(7): 272-273.
- Quilty, P.G., 1966: The Age of Tasmanian marine Tertiary Rocks. Aust. J. Sci. 29: 143-144.
- Raven, P.H. and D.I. Axelrod, 1972: Plate Tectonics and Australasian Paleobiogeography. Science 176: 1379-1386.
- Rensch, B., 1959: Evolution above the Species level. John Wiley and Sons Inc. New York.

- Rich, P.V., 1975: Antarctic Dispersal Routes, Wandering Continents, and the Origin of Australia's Non-Parseriform Ovifauna. Men. Nat. Mus. Vic. 36: 63-125.
- Ride, D.L., 1956: The affinities of *Burramys Parvus* Broom a fossil phalangeroid marsupial. Proc. Zool. Soc. Lond. 127: 413-429.
- Ride, W.D.L., 1962: On the Evolution of Australian Marsupials. In the Evolution of living Organisms (O.W. Leeper ed.) Melb. Univ. Press.
- Ride, W.D.L., 1964(a): A review of Australian Fossil Marsupials Jour. Roy. Soc. West. Aust. V. 47: 97-131.
- Ride, W.D.L., 1964(b): A list of mammals described from Australia between the years 1933 and 1963. Supplement to Australian Society Bulletin No. 7.
- Ride, W.D.L., 1967: On *Scepharnodon ramsayi* Owen 1884: The selection of a Lectotype, the clarification of its type locality, and on its identity with *Phascolonus gigas* (Owen 1859). Rec. S. Aust. Mus. 15: 419-426.
- Ride, W.D.L., 1968: On the past present and future of Australian Mammals. Aust. J. Sci. V. 31: 1-18.
- Ride, W.D.L., 1970: A guide to the nature mammals of Australia. Oxford Univ. Press, Melbourne.
- Rodger, J.C. and R.L. Hughes, 1963: Studies of the accessory glands of male marsupials. Aust. J. Zool. 21: 303-320.
- Romer, A.S., 1966: Vertebrate Paleontology. University of Chicago Press, Chicago and London.
- Schaeffer, B., M.K. Hecht, N. Eldredge, 1972: Phylogeny and Paleontology. In *Evolutionary Biology* V. 6. p. 31-46. (Dolyhansky, T., M.K. Hecht and W.C. Steere, eds.) New York, Appleton Century Crafts.
- Sharman, G.B., 1961a: Embryonic Membranes and Placentation in Five Genera of Diprotodont Marsupials. Proc. Zool. Soc. Lond. 137: 197-
- Sharman, G.B., 1961b: The Mitatic Chromosomes of Marsupials and their bearing on Taxonomy and Phylogeny. Aust. J. Zool. 9: 38-59.
- Sharman, G.B., 1965: Marsupials and the Evolution of Viviparity. In *Viewpoints of Biology* Pt. 4. Carthy, J.D. and C.L. Duddington (Eds.) pp. 1-21. Butterworths, London.
- Sharman, G.B., 1970: Reproductive Physiology of Marsupials. Science 167: 1221 -
- Sharman, G.B., 1973a: The chromosomes of non-eutherian mammals. In *"Cytotaxonomy and Vertebrate Evolution"* pp. 480-530. London: Academic Press.
- Sharman, G.B., 1973b: Marsupial Taxonomy and Phylogeny. Aust. Mammalogy. 1: 137-154.

- Sharman, G.B., J.H. Calaby and W.E. Poole, 1966: Patterns of reproduction in female Diprotodont Marsupials. In Zool. Soc. Lond. Symp. 15. Ed. I.W. Rowlands. pp. 205-233. London Academic Press.
- Shotwell, J.A., 1955: An approach to the paleoecology of mammals. Ecology 36: 327-337.
- Simpson, G.G., 1930: Post Mesozoic Marsupialia "Fossilium Catalogues", Animalia Pars. 47. Ed. J.F. Pompecky (W. Sunk: Berlin).
- Simpson, G. G., 1941: The affinities of the Borhyaenidae. Am. Mus. Novits. 1118.
- Simpson, G.G., 1953: The Major features of Evolution, New York: Columbia University Press.
- Simpson, G.G., 1961(a): Principles of Animal Taxonomy. New York, Columbia University Press.
- Simpson, G.G., 1961(b): Historical Zoogeography of Australian Mammals. Ev. 15: 431-446.
- Simpson, G.G., 1970: The Agyrologidae, Extinct South American Marsupials. Bull. Mus. Comp. Zool. V, 139, No. 1.
- Slaughter, B.H., 1968: Earliest known marsupials. Science 162: 254-5.
- Slaughter, B.H., 1971: Mid-Cretaceous (Albian) therians of the Butler Farm local fauna Texas. In Early Mammals (Kermack, D.M. and K.A. Kermack, eds.) p. 131-143. London, Academic Press Inc. Ltd.,
- Smith, J.M.B., 1974: Southern Biogeography on the Basis of Continental Drift: A Review. Aust. Mammalogy 1(2): 213-221.
- Smith, R.F.C., 1968: Studies on the Marsupial Glider Schinobates volans (Kerr), 1. Reproduction. Aust. J. Zool. 17: 625-636.
- Smith, A.G., J.C. Bridon and G.E. Drewry, 1973: Phanerozoic World Maps. In Organisms and Continents through time Symposium of Paleontological Assoc. London, Hughes, F (ed.), Special Papers in Paleontology No. 2.
- Sonntag, C.F., 1922: On the myology and classification of the wombat, koala and phalanger. Proc. Zool. Soc. London for 1922, pp. 863-869.
- Spencer, B., 1900: A description of Wynyardia bassiania, a fossil marsupial from the Tertiary beds of Table Cape, Tasmania. Proc. Zool. Soc. Lond. 776-795.
- Stephenson, N.G., 1964: On fossil giant wombats and the identity of Siepornodon ramsayi. Proc. Zool. Soc. Lond. 142: 537-546.

- Stephenson, N.G., 1967:; Phylogenetic Trends and Speciation Among Wombats. Aust. J. Zool. 15: 873-80.
- Stirton, R.A., 1955: Late Tertiary Marsupials from South Australia. Rec. South Aust. Mus. 11: 247-268.
- Stirton, R.A., 1955: Late Tertiary marsupials from South Australia. Rec. S. Aust. Mus., 9(3): 247-268.
- Stirton, R.A., 1957: Tertiary Marsupials from Victoria, Australia. Mem. Vict. Nat. Mus. 21: 121-134.
- Stirton, R.A., 1957b: A new Koala from the Pliocene Plankarinna fauna of South Australia. Rec. S. Aust. Mus. 13(1): 71-82.
- Stirton, R.A., 1963: A review of the macropodid genus *Protemnodon*. Univ. Calif. Publ. Geol. Sci., 44(2): 72-162.
- Stirton, R.A., 1967a: The Diprotodontidae from the Ngapakaldi fauna, South Australia. Bull. Bur. Min. Res. 85: 1-4.
- Stirton, R.A., 1967b: A diprotodontid from the Miocene Kutjamarpu fauna. Bull. Bur. Min. Res. 85: 45-51.
- Stirton, R.A., 1967c: A new species of *Zygomaturus* and additional observations on *Meniscolophus* Pliocene Palankarinna fauna, South Australia. Bull. Bur. Min. Res. No. 85: 129-147.
- Stirton, R.A., R.H. Tedford and A.H. Miller, (1961: Cangoic stratigraphy and vertebrate paleontology of the Tirari Desert, South Australia. Rec. S. Aust. Mus. 14: 19-61/
- Stirton, R.A., M.O. Woodburne and M.D. Plane, 1967: Tertiary Diprotodontidae from Australia and New Guinea: Bull. Bur. Min. Res. Geol. and Geophys. No. 58.
- Stirton, R.A., M.O. Woodburne and M.D. Plane, 1967: A phylogeny of the Tertiary Diprotodontidae and its significance in correlation. Bull. Bur. Min. Res. No. 85: 149-160.
- Stirton, R.A., R.H. Tedford and M.O. Woodburne, 1967: A new Tertiary formation of fauna from the Tirari Desert, South Australia. Rec. S. Aust. Mus. 15: 427-462.
- Stirton, R.A., R.H. Tedford and M.O. Woodburne, 1968: Australian Tertiary deposits containing terrestrial mammals. Univ. Calif. Publ. Geol. Sci. V. 77.
- Tate, G.H.H., 1947: On the Anatomy and Classification of the Dasyuridae (Marsupialia). Results of the Archbold Expedition No. 56. Bull. Am. Mus. Nat. Hist. V. 88: 103-155.
- Tate, G.H.H., 1945(a): The Marsupial Genus *Phalanger*; Results of the Archbold Expeditions No. 52. Am. Mus. Nov. 1283.

- Tate, G.H.H., 1945(b): The marsupial genus *Pseudochierus* and its subgenera - Results of the Archbold Expedition No. 54. Am. Mus. Nov. 1287.
- Tate, G.H.H., 1945(c): Notes on the squirrel-like and Mouse-like Possums (Marsupialia). Results of the Archbold Expedition No. 55. Am. Mus. Novit. 1305.
- Tate, G.H.H., 1948(a): Studies on the Anatomy and Phylogeny of the Macropodidae (Marsupialia). Results of the Archbold Expedition No. 59. Bull. Am. Mus. Nat. Hist. 91: 237-351.
- Tate, G.H.H., 1948(b): Studies in the Peramelidae. Bull. Am. Mus. Nat. Hist. 92. 317-346.
- Tedford, R.H., 1955: Report on the extinct mammalian remains at Lake Menindee, N.S.W. Rec. S. Aust. Mus. 11: 299-305.
- Tedford, R.H., 1966: A review of the Macropodid Genus *Sthenurus* Univ. Calif. Publ. Geol. 57. 1-72.
- Tedford, R.H., 1967a: Fossil mammals from the Carl Creek Limestone, Northwestern Queensland. Bull. Bur. Miss. Res. No. 92.
- Tedford, R.H., 1967b: The fossil Macropodidae from Lake Menindee N.S.W., Bull. Dept. Geol. Univ. Calif. 64: 1-156.
- Tedford, R.H., M.R. Banks, N.R. Kemp, I. McDougal and F.L. Sutherland 1975: Recognition of the oldest known fossil marsupials from Australia. Nature, 255. pp. 141-142.
- Troughton, E. LeG., 1959: The marsupial fauna, its origin and radiation. Pp. 69-88 in "Biogeography and ecology in Australia" ed. A. Keast et al (Junk: The Hague).
- Turnbull, W.D., 1971: The Trinity Therians: Their Bearing on Evolution in Marsupials and Other Therians. In Dental Morphology and Evolution. A. Dahlberg (ed.) pp. 151-179. University Press, Chicago.
- Turnbull, W.D. and Sundelius E.L., 1970: The Hamilton fauna. A late Pliocene Mammalian fauna from the Grange Durn, Vic. Aust. Fieldiana, Geology 19: 1-163.
- Turnbull, W.D. and F.R. Schram, 1973: Broom Cave *Cercartetus*, with observations on Pygmy Possum Dental Morphology, Variation and Taxonomy. Rec. Aust. Mus. Syd. 28(19): 437-464.
- Tyndale-Biscoe, G.H., 1966: The Marsupial Birth Canal. In Zool. Soc. London. Symp. 15 (Ed. I.W. Rowlands) pp 233-250 Lond. Academic Press.
- Tyndale-Biscoe, H. 1973: Life of Marsupials. E. Arnold. London.
- Van Deuson, H.M., 1964: First New Guinea record of *Thylacinus*. J. Mammal. 44: 279-280.

- Van-Valen, L. 1969: Evolution of Dental Growth and Adaptation in Mammalian Carnivores. Av. 23: 96-117.
- Van-Valen, L. 1971: Adaptive zones and the orders of Mammals. Av. 25: pp. 420-428.
- Wakefield, N.A., 1963: The Australian Pigmy Possums. Vict. Nat. Mus. 80: 99-116.
- Warren, J.W., 1965: Description of a fossil numerus (Marsupialia) from the lower Pliocene of Victoria, Australia. Proc. Roy. Soc. Vict. 79: 147-151.
- Weller, J.M., 1969: The Course of Evolution. McGraw Hill, U.S.A.
- Wilson, E.O., 1965: A consistency test for phylogenies based on contemporaneous species. Synt. Zool. 14: 214-220.
- Wood, H.E., 1924: The position of the "sparassodonts" with notes on the relationships and history of the marsupialia. Bull. Amer. Mus. Nat. Hist. LI: 77-101.
- Woodburne, M.O., 1967a: Three new diprotodontids from the Tertiary of the Northern Territory Australia. Bull. Bur. Min. Res. 85: 53-103.
- Woodburne, M.O., 1967b: The Alcoala Fauna, Central Australia, An Integrated Paleontological and Geological Study: Bull. Bur. Min. Res. Geol. and Geophys. No. 87.
- Woods, J.T., 1958: The extinct genus Palorchestes. Mem. Q. Mus. 13(4): 177-193.
- Woods, J.T., 1961: The skull of Thylacaleo. Mem. Q'ld. Mus. 13(2): 125-140.
- Woods, J.T., 1962: Fossil Marsupials and Cainozoic stratigraphy in Australia: A review. Mem. Q'ld. Mus. 14(2): 41-49.
- Yadov, M., 1973: The Presence of the Cervical and Thoracic Thymus lobes in Marsupials. Aust. J. Zool. 21: 285-301.
- Yunis, E., J. Cayon and E. Ramirez, 1973: The Chromosomes of Metachirus nudicaudatus (Marsupial: Didelphidae). Aust. J. Zool. 21: 369-73.
- Ziegler, A.C., 1971: A theory of the Evolution of Therian dental formulas and Replacement Patters. Q'ld. Rev. Biol. 46: 226-249.
- Ziegler, A.C., 1972: Guide to Native land Mammals of Northeast New Guinea.